CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS

III. STIPITOPTERIS

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The fossil described in this paper, a fern petiole fragment referable to the form genus *Stipitopteris,* was discovered in a coalball collected at the Pyramid Mine of the Binkley Coal Company, located three miles south of Pinckneyville in Perry County, Illinois. The coal in this mine is described as belonging to the lower McLeansboro series and is known as coal number 6. A more detailed discussion of the occurrence of coal-balls at this locality has been given in the first of this group of contributions (Andrews, '42).

Materials and Procedure.—The single specimen of this fern consists of a fragment of a petiole approximately 4 cm. long. The coalball containing it, numbered WBC170 in the collections of the Henry Shaw School of Botany of Washington University, was cut into six sections, each being approximately 13 mm. in thickness. The fern petiole was well preserved in the two center sections, but rather badly crushed and distorted in the two adjoining ones. Of the center sections, one was used to prepare a series of transverse peels while the other was used for longitudinal sections. It was possible in this way to observe the nature of the tracheid pitting as well as the distinctive transitional anatomy of the trace as a whole.

The nitrocellulose peel method was used in obtaining preparations. This method produced much more satisfactory preparations for study and photographic purposes than ground sections, chiefly

because the dark contents in the parenchyma cells of the latter made it very difficult to grind sections sufficiently thin.

Description.—The petiole is more or less oval in outline and measures approximately 10 by 13 mm. in diameter. The most distinctive feature is the transitional organization of the xylem of the leaf trace. At one end of the specimen (pl. 9, fig. 1) the trace is in the form of an elongated "horseshoe" with the free ends involuted, while at the opposite end (fig. 4) it forms a continuous band enclosing an isolated W-shaped segment. A selection from the peel preparations shows these extremities as well as two intermediate stages (figs. 3, 4) in the isolation of the W-shaped strand. Text-figures 1 and 2 show the organization of the xylem tissue of the leaf trace as reconstructed from the series of peel preparations. The actual distance through which the illustrated transition takes place is approximately 10 mm. The longitudinal dimension has been exaggerated somewhat in the text-figures in order to show the transition clearly.

The xylem of the trace, which is shown as the rather prominent white band in figs. 1-4, consists of primary metaxylem 2–4 cells wide with scattered groups of protoxylem located on the inner side. The metaxylem cells are uniformly scalariform (pl. 10, fig. 7) and vary from 15 to 91μ in transverse section, the average being about 47μ.

The protoxylem groups are endarch and numerous, being arranged around the entire inner periphery of the metaxylem, although they are more numerous in the involuted portion of the trace (fig. 1). It is difficult to ascertain the exact number of protoxylem groups, partly because of faulty preservation in spots and partly because the size distinction is not always great between metaxylem and supposed protoxylem. The number is approximately 25–30 and the average size of a clearly defined protoxylem cell is 21μ. In the isolated W-shaped strand they are found on the upper side, as the petiole is illustrated in fig. 3. This corresponds to the inner side of the surrounding cylinder.

Scott ('09), in describing the protoxylem of *Caulopteris,* does not mention the number of protoxylem groups present but only says that they occur, "as a number of small groups of cells on the inner edge of the xylem, which is thus endarch" [page 302]. This agrees with the specimen described here which has been shown to have centrally located protoxylem groups.

Phloem, pericycle and endodermis are not preserved. In all our

preparations the inner cortex is rather closely appressed to the xylem although there is some evidence that a tissue (or tissues) was formerly present between them. If such were the case it must have been a very narrow layer.

The cortex presents a number of distinctive features. Taken as a whole, it is composed of two sharply defined zones. The outer one reaches a thickness of a little more than 1 mm. and consists of cells which are large, thin-walled and rather badly crushed due to their apparently delicate nature in life. The inner zone averages about 1.5 mm. thick and consists of somewhat smaller cells partially filled with an opaque substance which may represent metamorphosed tannin or gum deposits. These two zones are separated by a narrow band of dark brown, closely compacted cells suggestive of meristematic activity. The pith or central parenchymatous mass consists of isodiametric cells with some dark contents but these are not so abundant as in the inner cortex.

Taxonomy.—There is little doubt that this petiole belongs to a stem of one of the Carboniferous tree ferns known from structually preserved remains as *Psaronius* and it evinces leaf scars of the *Caulopteris*[1] type. This is evident from a comparison of the Illinois specimen as shown in figs. 1–4 with *Caulopteris varians* Renault and Zeiller ('88) (pl. 10, fig. 5). The portion of the stem of *C. varians* in Renault and Zeiller's figure shows leaf scars at slightly different levels, and since the transition of the leaf trace takes place rapidly the comparison is possible. One of the bundle scars shown in their figure presents the elongated horseshoe type of trace similar to that in the Illinois specimen shown in pl. 9, fig. 1. Another bundle scar on the same portion of the stem shows the trace as a continuous band with the isolated W-shaped segment within the outer band (c.f. pl. 9, fig. 4).

Since the petiole described here was not found attached to the stem of *Caulopteris,* though there is little doubt that it was originally, it becomes necessary to describe it under the name *Stipitopteris.* That genus was introduced by Grand'Eury in 1877 for petioles of ferns whose structure in cross-sections corresponds to the marks on the leaf scars of *Caulopteris,* but which were not known in organic connection with the latter.

The leaf scars of certain species of *Stemmatopteris* Corda, de-

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[1] The name *Caulopteris* was first used by Lindley and Hutton ('32) for supposed stems of the tree fern *Psaronius* which had been preserved as casts showing only surface features.

scribed by Lesquereux ('80) from the Carboniferous formation of Pennsylvania, show a similarity to a cross-section of the petiole described in this paper. *Stemmatopteris* and *Caulopteris* are undoubtedly closely related or even congeneric, and Lesquereux himself wrote that "the whole number of our species could have been described without inconvenience under the name of *Caulopteris.*" Hirmer ('27) considers the two congeneric.

There is also a striking similarity between the petiole described here and species of the genus *Anachoropteris* Corda. Darrah ('41), in his recent account of the Coenopterid ferns of the American coalballs, points out that the taxonomic limits of *Anachoropteris* are in considerable doubt and that some of the forms included in the genus are now known to be portions of plants really belonging to other genera. He states, however, that the involute stele of most of the species seems to constitute a generic character. Corsin ('37), in his treatment of *Anachoropteris,* speaks of the protoxylem as occurring on the outside of the metaxylem rather than on the inside as in *Stipitopteris.* This apparent difference, in conjunction with the similarities between both of the aforementioned genera, brings up the question of the taxonomic value of the location of the protoxylem. Tansley and Lulham ('05) considered that in many cases it is of considerable significance, and they point out the universal exarchy of the steles of the Sphenophyllales and Lycopodiales and the endarchy of the Angiosperms. However, they conclude that the Filicales are rather different in that the exact position of the spiral protoxylem in relation to the metaxylem of the vascular strands of the stem is decidedly variable. They found exarchy, endarchy and mesarchy all within comparatively small groups, and concluded that the actual course of evolution seems to affect the position of the protoxylem much more freely and rapidly than in the other great groups of vascular plants. From this evidence it would seem that the use of the location of the protoxylem to separate genera in this group of ferns might be questioned. It is, however, evident that the stability of this character varies in different groups.

It is probable that an extensive taxonomic revision of the genera *Anachoropteris, Caulopteris, Stipitopteris* and *Psaronius* will be necessary in the future. This paper is intended as a further contribution to the apparent relationship between petioles described as *Anachoropteris* and *Stipitopteris* and fern stems described as *Psaronius* and *Caulopteris.*

STIPITOPTERIS

Grand'Eury ('77) described four species of *Stipitopteris* from the Carboniferous of France. His descriptions are very brief, and his only illustration is the cross-section of a petiole which is merely labeled *Stipitopteris*. It is interesting to note, however, that the isolated strand of xylem in his specimen is turned in the exact opposite direction from the Illinois specimen. Since the Illinois specimen is quite distinct from any described species of *Stipitopteris* it is described here as a new species.

Stipitopteris americana Lenz, sp. nov.—Petioles somewhat oval, 10 by 13 mm. in diameter; cortex consisting of two distinct zones, the outer approximately 1 mm. in thickness and formed of cells which are large, thin-walled and rather badly crushed, the inner about 1.5 mm. in thickness and consisting of somewhat smaller cells partially filled with an opaque substance; zones separated by a narrow band of dark closely compacted cells; leaf trace in the form of an elongated horseshoe with the ends involuted and fusing to form an isolated W within a continuous xylem cylinder; protoxylems endarch, of spirally thickened tracheids in small scattered groups; metaxylem 2–4 cells thick, consisting of scalariform-pitted tracheids, 15–91 µ in diameter.

Locality: Pyramid Mine of the Binkley Coal Company, Perry County, Illinois.

Type: Coal-ball WCB170 in the collections of the Henry Shaw School of Botany of Washington University.

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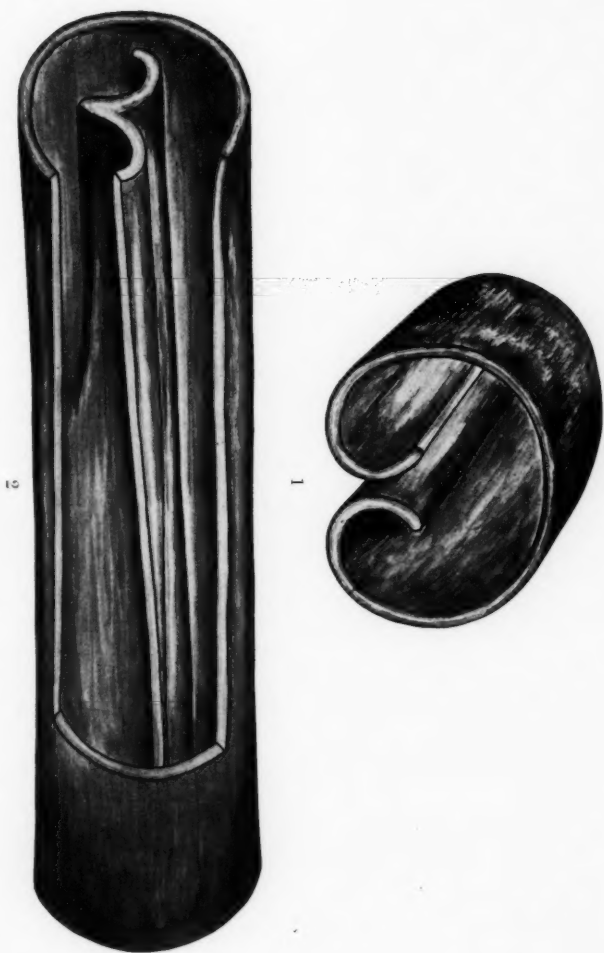
Text-figs. 1, 2. *Stipitopteris americana.* Reconstruction from a series of peels showing the transition of the xylem tissue from the horseshoe shape, shown in fig. 1, to the cylinder of xylem enclosing the isolated W-shaped segment, shown in fig. 2.
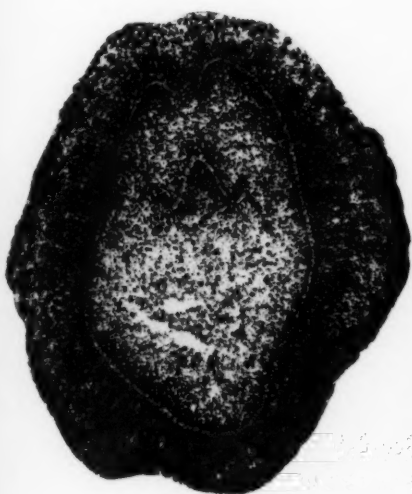
EXPLANATION OF PLATE

PLATE 9

Figs. 1–4. *Stipitopteris americana.* Part of a series of peel preparations showing the transitional anatomy of leaf trace; fig. 1, WCB170D.B9, fig. 2, WCB170D.T40a; fig. 3, WCB170D.T25; fig. 4, WCB170D.T8. All figures × 5.
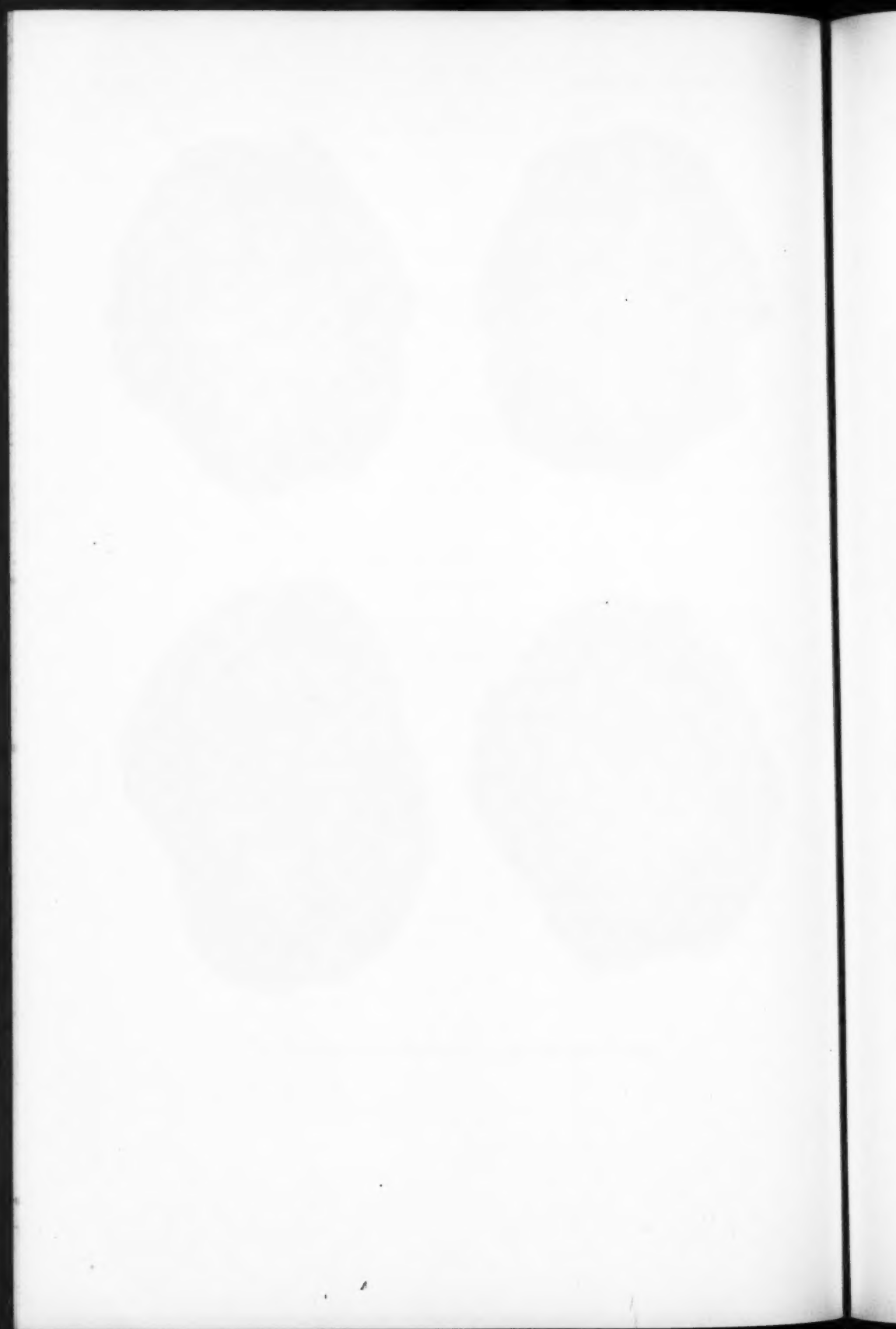
PLATE 9

LENZ—AMERICAN CARBONIFEROUS FLORAS. III

Explanation of Plate

PLATE 10

Fig. 5. *Caulopteris varians* Renault and Zeiller. From Renault and Zeiller ('88).

Fig. 6. *Stipitopteris americana* Lenz. Longitudinal section showing the spirally thickened tracheids of the protoxylem; WCB170C.S18, × 110.

Fig. 7. *Stipitopteris americana* Lenz. Longitudinal section showing the scalariform-pitted tracheids of the metaxylem; WCB170C.S21, × 110.

Plate 10

LENZ—AMERICAN CARBONIFEROUS FLORAS. III

RACES OF ZEA MAYS: I. THEIR RECOGNITION AND CLASSIFICATION[1]

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It is now half a century since E. Lewis Sturtevant ('85, '86, '87, '94, '99) reviewed the variability of *Zea Mays* and catalogued it in six main groups, five of which were based upon the composition of the kernel. There are now available two new kinds of facts in addition to those which were at his disposal. In the first place, archeological research has made great advances and the museums of this country have numerous collections of prehistoric corn, the best of them in a remarkable state of preservation, their age approximately dated by dendrochronology (Guernsey and Kidder, '21). In the second place, the rise and development of corn genetics have provided us with a large body of technical information concerning the relationships of different kinds of corn. We know, for instance, that the change from flint corn to flour corn is controlled by a single gene difference, whereas the change from a flint to a dent is the result of many genes, so that in working out the relationships of corn the difference between flint and flour is trivial compared to the difference between flint and dent.

Mangelsdorf and Reeves have recently ('38, '39) advanced a new theory as to the relationships between corn and its closest relatives. For the examination of this hypothesis, or of any hypothesis dealing with the history of corn, it is important that the classification of the varieties of maize be re-examined in the light of our present knowledge of their history and relationships. For this purpose Sturtevant's classification has another disadvantage in addition to the fact that it does not incorporate the modern evidence. It is largely *artificial* rather than *natural,* as he himself was well aware ('94, p. 320).

It is not only in the classification of maize that one has to choose between these two methods, the natural and the artificial. Which to choose is one of the fundamental problems of all attempts at classification. Each method has its advantages and disadvantages. An artificial classification is an efficient catalogue and nothing more; it sets up a comprehensive series of pigeon-holes. A natural classification attempts in addition to put closely similar objects in adjacent pigeon-holes. An artificial classification may be simple, objective, rapid and complete, but it tells us little more than the pigeon-hole number of the catalogued object. A natural classification is often difficult, incomplete, and more or less subjective, but in addition to cataloguing an object it tells something about what *kind* of an object it is.

In most taxonomic work natural classifications are seldom attempted within the limits of a species or sub-species. Though a monographer may often realize that the individuals which he is lumping together as one species are grouped into more or less well-defined natural races, nevertheless he seldom has the time or the special training for attempting *intra*-specific classification. But though the problem may be difficult it cannot be ignored by those who work with man or domesticated plants and animals. While, for such problems, a wholly natural classification would be desirable, a more or less artificial one usually has to be adopted for practical reasons. In dealing with the people of a community, for instance, the telephone company lists them alphabetically. Like any good artificial classification, the telephone book is complete, objective, and requires no special training either to make or to use. It is convenient but it does not put similar people in adjacent positions. The O'Connors find themselves next to the Ochsners and the Cabots to the Cabrilliacs. When a sociologist studies the same community he might like to have a complete natural classification in which the O'Connors would go near the Kellys, and the Cabrilliacs with the Oldanis. In practice he must be satisfied with a few large natural groupings such as nationality, occupation, income, etc. Anything more elaborate than this is seldom put down on paper because it is too difficult.

Sturtevant's classification of corn was both artificial and natural, principally the former. It had six main subdivisions. One was pod corns. The other five considered only the composition of the kernel: the pop corns, the flint corns, the dent corns, the flour corns, and the sweet corns. To the extent that any two corns with the same kind

of kernel are by that very fact somewhat alike, it did put similar kinds of maize together. On the other hand, as Sturtevant himself pointed out, by ignoring other features of the maize plant, it often separated varieties which naturally belonged together. This system had exactly the advantages and the disadvantages of a classification of mankind based entirely on hair color. Such a classification would be rapid and complete and would, to a certain extent, group like peoples together, but it would separate a black-haired Norwegian from his fair-haired relatives and put him in the same class with Sicilians and gypsies.

The problem of races and their recognition is indeed almost the same in *Zea Mays* as in mankind. In both cases it is not easy to work out the racial composition of the whole and it is difficult to give a precise definition to the term "race." The latter problem has been discussed by Coon ('39) in the introduction to his book on the races of Europe:

"Since man is the oldest domestic animal . . . any attempt to classify him by a rigid scheme is immensely difficult and the scheme must be elastic if it is to work at all. Hence the term 'race' must also be elastic. We may recognize if we like, certain major races of the Old World such as the Bushman-Hottentot, the Pygmy, the Australoid, the Negro, the Mongoloid, and the White. Within each of these major racial groups there are, or have been, smaller entities, which may deserve the designation of race in a lesser sense. These smaller entities consist, for the most part, of groups of people reasonably isolated, and developing into local physical enclaves. . . . At what border point such an entity becomes a major race it is not always possible to say."

For the classification of *Zea Mays* we shall define the word race as loosely as possible, and say that a race is a group of related individuals with enough characteristics in common to permit their recognition as a group. The last three words should be emphasized. As Hooton has said in his discussion ('26) of racial analysis, "races are great groups and any analysis of racial elements must be primarily an analysis of groups, not of separate individuals. One must conceive of race not as the combination of features which gives to each person his individual appearance, but rather as a vague physical background, usually more or less obscured or overlaid by individual variations in single subjects and realized best in a composite picture."

From the standpoint of genetics a race is a group of individuals with a significant number of genes in common, major races having a smaller number in common than do sub-races. The degree to

which a species can be divided into recognizable races and sub-races will depend upon the degree to which it has been divided into distinct intra-breeding groups with distinctive combinations of genes.

In the recognition of race in *Zea Mays* it is therefore essential that we rely upon characters with a broad genetic background (such as cob shape and kernel size) rather than those which are indicators of but a single locus (as starchy vs. sweet or flint vs. flour). A natural classification of the races of *Zea* based upon characters like cob shape, kernel size, and tassel type will be incomplete, and one must expect disagreement as to details, even among authorities. For some time to come it must be a goal to work towards rather than a project to be completed. As a basis for understanding the history and genetics of corn, it is worthy of such long-continued effort. Since it is an attempt at a classification based upon the entire germ-plasm, it will integrate the maximum number of genetic facts.

This does not mean that the races defined in this paper will supplant Sturtevant's classification as a cataloguing device. Any large enumeration of the varieties of corn must still be indexed by his system or by some such artificial system, though eventually some of the features of a natural system should be worth incorporating in a new comprehensive classification. For that reason no Latin names or precise diagnoses are given to the races of corn tentatively recognized in these papers. We have instead given short descriptive names to some of those groups of varieties in our collections with a recognizable core of common features.

A person who is acquainted with *Zea Mays* only in one section of the world will be amazed at a collection of varieties from another region. In the United States, for instance, maize is so variable that one who has not seen it elsewhere would think that it could not ever be much more variable. Yet a collection from a single Mexican state will show at least one and sometimes two or three new races. Each will have a variability of its own and will differ from the maize of the American corn belt. A discussion of the North American races of *Zea Mays* must therefore begin with a description of its total variability, with special reference to those features which distinguish the maize of one region from that of another.

A SURVEY OF INTER-RACIAL VARIABILITY IN MAIZE

For purposes of description (see Weatherwax, Chapters v–ix, xiv–xv) we may divide a plant of *Zea Mays* into root and shoot. The

shoot consists of a primary axis, which often gives rise to secondary axes at its base. The primary axis is composed of a variable number of nodes with a leaf at each, and is prolonged into a compound male inflorescence, commonly called the tassel. At one or more of the nodes, short secondary branches arise with short wide foliar organs (the husks) and terminated by a condensed compound female inflorescence (the ear). Smaller ears arise in the axils of these foliar organs but they seldom develop to a functional stage.

Root.—

Though variation in the root is not as conspicuous as that in the shoot, it certainly exists (see Collins, 1918). Some Mexican and southwestern races of corn have much longer mesocotyls and many of the varieties of the Mexican plateau have poorly developed root systems as reported by Kuleshov ('30). We have not as yet been able to work out any standardized measurement of these characters which can be used as a criterion of race.

Branching of the Primary Axis.—

The degree of branching of the primary axis and the relative development of the primary and secondary axes vary greatly in different races of corn. They are so unlike in the same variety of corn when it is planted in widely separated localities or at different times of year that we have not found it practicable to use this character as a criterion. The proportionate development of primary and secondary axes (stalk and tiller) is a more stable character and, with a little more study, might be found useful.

Node Number and Internode Length.—

Races of corn differ significantly in node number, but it is too affected by the environment to be useful as a racial criterion. The fundamental pattern of internode length is perhaps more stable and with a little further study might be found useful. Figure 1 shows the pattern of internode lengths in four different races of corn. It will be seen that there are considerable differences in the degree to which the internodes lengthen immediately above the uppermost ear.

Leaves (Blade and Sheath).—

The leaves of the various races differ greatly not only in their absolute size but in their proportions, as has already been commented upon by Kuleshov (loc. cit.). There is so much variabil-

ity upon each plant that we have not been able to determine an efficient method of scoring leaf shape. The leaf sheaths differ in their hairiness from race to race, and this we have been able to score in three qualitative grades, slight or none, evident, and heavy.

Male Inflorescence.—

The tassel of *Zea Mays* presents us with more easily measured characters than all the rest of the plant combined. While the homologues of its variation are present in the ear, the mature cob is so grown together and lignified that it is difficult to dissect and recognize the component parts.
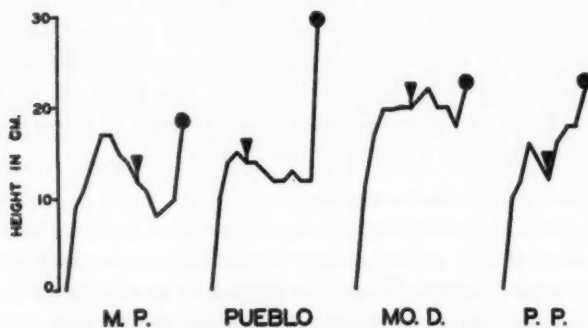

Fig. 1. Successive internode lengths for representative plants of Mexican Pyramidal, Pueblo, a dent corn from Missouri, and Pima-Papago. All grown out-of-doors at St. Louis. Circles represent tassels, and triangles represent ears.

The tassel is composed of a central axis and a varying number of secondary axes, the lowest of which are themselves compound (Weatherwax, pp. 100–102). The spikelets tend very strongly to be arranged in pairs, one sessile and one pedicellate. The spikelet pairs are arranged distichously upon the secondary axes and polystichously upon the central spike. Although all these features are subject to variation, the general plan remains remarkably constant in different races of corn. The number of tassel branches is a surprisingly stable character (Weatherwax, p. 102) and is one of the most useful criteria of race. To be sure, it is a character which is affected by the vigor of the plant and for that reason we did not consider using it until experience forced its general stability upon our attention. It was first brought to our notice in connection with Cutler's collections of maize from the Mexican Plateau for which we had (1) tassels collected in the Mexican corn fields, (2) tassels

grown in the greenhouse at St. Louis, (3) tassels from corn started in the greenhouse and ripened out of doors, (4) corn planted out of doors in St. Louis in May. While for each of these four lots the material was variable, the variation in each was from 0 to 4 branches. At the same time we also had in cultivation corn from Guatemala which bore a very large number of tassel branches though planted at the same time and in adjacent rows.

It was also found to be generally true that the range of variation in number of tassel branches was roughly the same for those cultures grown in triplicate at College Station, Cuba, and St. Louis (see pl. 11, tassels D and E).

In one characteristic Mexican race there are no branches or only a few, while in South American corns there may be 30 or more branches. The stiffness of the entire tassel and the angle at which its branches depart from the primary axis is useful in the field but we have not been able to score it effectively on herbarium specimens. The size of the outer glumes of the spikelet is also important. It varies from 8 or 9 mm. in some South American corns to 15 or 16 mm. in corn from the Mexican plateau. The length of the sterile zone at the base of the branches is also significant. This varies from 1 or 2 mm. in some Mexican corn to 10 or 20 mm. in certain South American varieties. Two technical characters are highly diagnostic of certain races, the condensation of internodes and the degree to which the pedicel on the upper spikelet is developed. In Peruvian corn successive internodes are equal in length and exhibit a characteristic, regular zigzag arrangement. In many North American varieties the internodes vary in length and are often so short that the spikelets appear as if borne four at a node. Two successive nodes may be so close together that they appear as one. In the corns of the Mexican plateau this condensation is sometimes quite regular, every second internode being condensed (fig. 2).

The spikelets, as has been said, occur in pairs, the upper spikelet of each pair being more or less pedicellate. The relative length of this pedicel varies greatly, however. In some South American corns it may be as long as the spikelet. In many Mexican corns it is sub-pedicellate and may even be quite as sessile as the lower spikelet. Plate 11 A shows an extreme example, a corn from Xochimilco in which all the spikelets are sessile and the alternate internodes condensed so that it has the appearance of bearing spikelets in whorls of four.

Female Inflorescence.—

Next to the tassel the most important criteria of race are to be found in the female inflorescence (the ear). The number of husks and their shape are highly diagnostic but we have not used it because ears with husks attached are difficult to store and to study. Ear and kernel were the basis of Sturtevant's classification and we have merely selected those of his criteria which seemed most diagnostic;

Fig. 2. Portions of tassel branches, greatly enlarged: left *Mangelsdorf 128852,* from Quinta, Peru; right, *Cutler 45,* from Xochimilco, Mexico.

row number, ear length, kernel width, thickness and length, and cob width. The composition of the kernel is an important racial criterion only to the extent that it is based upon a large number of genes. Starchy vs. sweet or flint vs. flour are simple gene differences and therefore of minor importance. Denting and capping, on the other hand, are the results of larger numbers of genes and are therefore more important though they are difficult to measure. Color differences, for the most part, are the results of a few gene differences and are somewhat superficial. However, it will be seen that when the races of maize have been separated on other grounds that each has its own characteristic color range.

In addition to these readily scored features, there are a number of general differences in ear shape, kernel pattern and kernel texture which are easily perceived by the trained eye but which are difficult to score objectively and commensurately (i.e., in a graded series). These include: (1) the general shape of the cob, cylindrical, long-tapering, short-tapering, (2) the shape of the butt, appressed, rounded or enlarged, (3) the extent to which the kernels are arranged in evident rows, (4) the sulci between the rows, (5) the regularity of the kernels (i.e., the amount of variation in size and shape from kernel to kernel), (6) the degree to which the kernels have been compressed by the husks.

The general problem of recognizing and measuring races has been discussed by Hooton ('26) in one of his classic contributions to the subject. Though he was considering mankind rather than *Zea Mays,* the problem is fundamentally the same and our techniques differ from his only in detail. Our material, however, had the advantage that we had two sets of complicated organs for analysis rather than one. His work was mainly limited to skulls. Ours had not only the ear but also the associated tassel. We followed his method in sorting out the ears by general perception, using the total impression given to the trained observer by its totality of characters. Having grouped his crania by this method, Hooton then measured them and computed averages for each recognized race, sub-race, etc. We had a somewhat better check on our conclusions since we first sorted the ears and then measured and averaged the associated tassels. In every case the exact *data* derived from the tassels confirmed our *judgments* with regard to the ears. Both of these conclusions received additional confirmation when the distributions of the races and sub-races were determined and were found to agree with recognized geographical and ethnic barriers. We had an added advantage in that much of our material was grown in triplicate at St. Louis, Mo., College Station, Texas, and Cienfuegos, Cuba, so that we had a rough idea of what differences were purely environmental. We are indebted to Dr. Paul C. Mangelsdorf and the Arnold Arboretum for the Cuban collections and to Dr. R. G. Reeves and the Texas A. and M. College for that grown at College Station.

The general method of work can be illustrated by our procedure with the collections from the southwestern United States. (These are to be discussed in greater detail in a forthcoming article by Anderson and Carter). For this area we had about fifty collections

made in the Southwest over a series of years by the junior author and by George F. Carter, to whom we are greatly indebted not only for a comprehensive collection but for much pertinent information. The tassels were collected and numbered by an assistant to reduce the personal equation to a minimum. The ears (some of them collected in the Southwest, others grown from seed collected there) were spread out on a large table and were carefully examined. It

GLUME LENGTH IN MM.

NO. TASSEL BRANCHES

% SUB-SESSILE SPIKELETS

% CONDENSED INTERNODE

LENGTH STERILE ZONE

————————— SMALL PIMA-PAPAGO
— — — — — LARGE   "   "
———— ---- ---- INTERMEDIATES
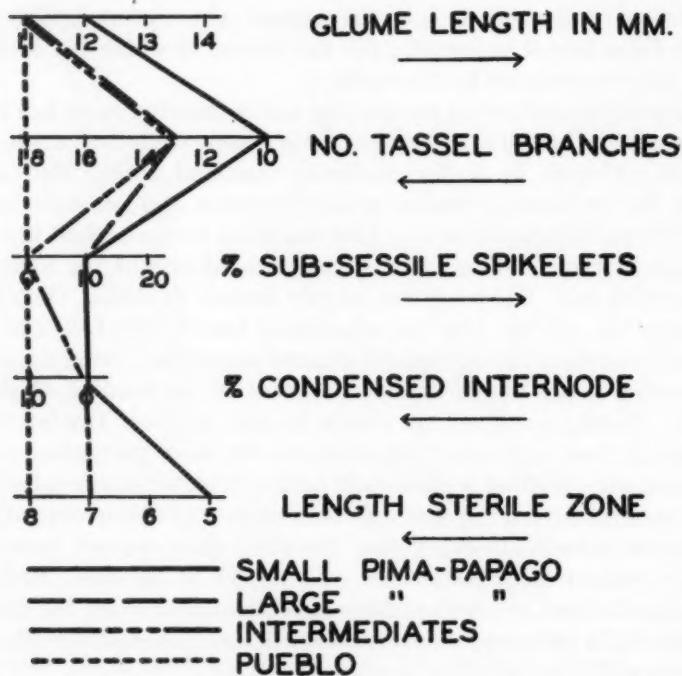---- ---- ---- ---- PUEBLO

Figure 3

was almost immediately apparent that there were at least two centers of variation: (1) the large-cobbed, straight-rowed varieties grown by the Pueblo Indians, and (2) the small-cobbed mosaic-seeded type grown by the Pima and Papago Indians. We therefore sorted the material into three piles, "Pueblo," "Pima-Papago," and unknowns. By study it was possible to reduce the third pile little by little and we soon came to the conclusion that, aside from a few obvious recent admixtures such as pop corns and dents, there were only these two basic races of corn in the Southwest. The ma-

terial lent itself to classification in four groups: (1) Pueblo, (2) obviously intermediate, (3) Pima-Papago, but somewhat intermediate, and (4) Pima-Papago. We then studied the numbered tassels and measured five features previously chosen as racially diagnostic. Averages for each of the four groups were then computed and are shown diagrammatically for all 5 characters in fig. 3. It will be seen that five measured characters of the tassels agree with our total impression of the ear and kernel. The Pima-Papago and Pueblo are extreme for each of the five tassel characters, the intermediates occupy an intermediate position, and the averages of class 3 depart only slightly from those of the Pima-Papago.

The distribution of these two races among the southwestern Indians was then examined and found to agree with geographical and ethnic barriers. The Pueblo varieties are grown by the pueblo-dwelling Indians of the plateaus, the Pima-Papago by the Indians inhabiting the intensely hot deserts near the delta of the Colorado. The Pima-Papago varieties are not grown at all by the eastern Pueblos and are found only among those western Pueblos (most particularly the Hopi) which have for some centuries been isolated from the main group of Pueblo Indians and which are geographically much closer to the territory of the Pima and the Papago.

After the classification of the southwestern maize had been completed the Mexican and Guatemalan collections were studied in the same way. For these areas, in addition to the material collected by Cutler, we had extensive collections which came to us through the courtesy of Prof. Carl Sauer and Prof. Ralph Beals of the University of California, and a small but extremely useful collection of tassels and associated ears made in Mexico by our colleague, Mr. R. W. Schery. For these areas our collections are not so comprehensive and the variation of *Zea Mays* is much more complex. There are undoubtedly numerous sub-races which we have not yet recognized and some of those which we are now recognizing may ultimately prove to be intermediates. They are put forward tentatively as a basis for the discussion that may eventually give us a comprehensive yet natural classification of the races of *Zea Mays*.

The three Central American races (or sub-races) which we are describing below under the names of "Guatemalan Big Grains," "Mexican Pyramidal" and "Guatemalan Tropical Flints" are advanced merely as a basis for study. Their relations to each other and to the other races of Central and South America remain to be

determined. They do not constitute the only races in our collections and it is not even suggested that the three groups are of the same rank. It is quite possible that when the racial composition of corn has been thoroughly worked out one of these three might constitute a major race and the other two would be of subordinate rank. Though all three are variable each one has enough of a core of common features and a definite enough distribution in space and time to be thought of as an entity.

In the southwestern United States the corn situation is simpler and we have much more comprehensive collections. The two races, "Pima-Papago" and "Pueblo," which we are describing below, are certainly the two main entities in the maize grown by the Indians of that region. Aside from the obvious intermediates discussed above, the only other perceptible influences are admixtures derived from the American and Spanish communities and various Mexican types brought in by Apache raids.

Mexican Pyramidal (fig. 4; pl. 11 A, B, C).—

This is the common corn of the region about Mexico City and was probably therefore closely associated with the Aztecs. It is so distinctive in leaf and habit that it was named *Zea hirta* over a hundred years ago by Bonafous (1836) and was described in detail by Kuleshov ('30), who called it the "central Mexican type" and described its pubescent leaf sheaths, drooping leaves, poorly branched tassels, and weak root systems. He also called attention to the fact that this type might have kernels which were pop or flour or dent "as well as any other form of maize." In addition to the characters described by Kuleshov, the Mexican Pyramidals have long harsh glumes in the tassel and a high percentage of condensed internodes and subsessile upper spikelets (pl. 11 and fig. 4). The ears are equally distinctive. Though varying greatly in size they all have the same general shape. They are relatively short and taper sharply and regularly, hence the name "Pyramidal." Row pattern varies from regular to irregular with mixtures of both being common. They most generally show little husk compression; there are wide spaces between the rows and often between individual grains. The kernels are prevailingly long though they vary in shape, usually on the same ear, pointed to dented to rounded kernels often occurring together. The kernel is nearly always elongated, however, and the denting is usually a slight depression towards the tip of the grain. White is the commonest color, accom-

panied by heavy white capping, but dark reds and blue-blacks are also met with.

This race is of particular importance not only because of its probable association with Aztec civilization but because it apparently has entered into the make-up of our corn-belt dents. Any one who will examine large fields of non-inbred dent corn can find (in a greatly reduced degree) much of the same variation which characterizes the ears and tassels of the Mexican Pyramidals. Many of the inbreds derived from dent corns exhibit in an exaggerated form certain of the characters to be found in Mexican Pyramidals though in any one inbred they are usually combined with other quite different features. The Mexican pop corns apparently form a subrace of the Mexican Pyramidals since in our material their tassels are indistinguishable and their cob shapes (as distinct from cob size) and kernel shapes are practically the same. More material must be examined before this conclusion can be accepted.
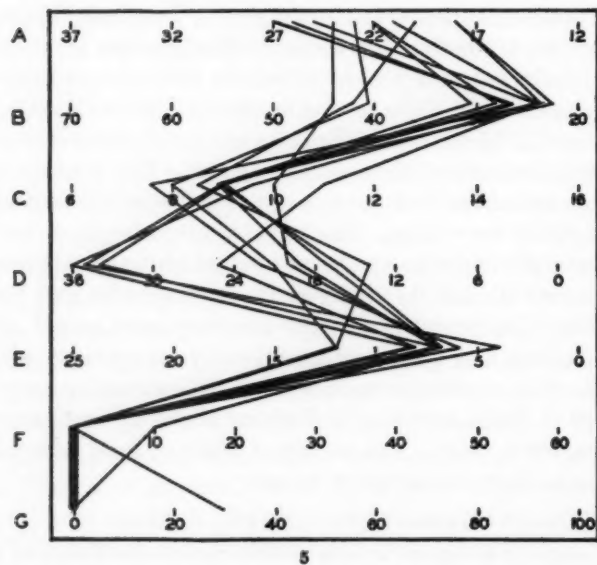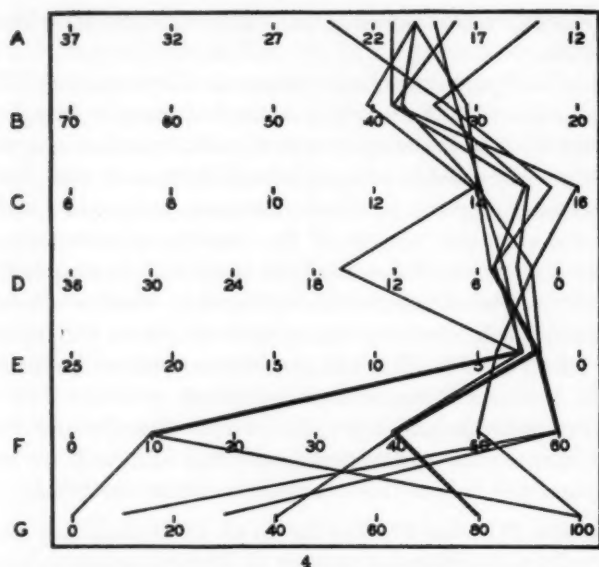
Guatemalan Tropical Flints (fig. 5; pl. 11 D, E, F).—

Apparently a considerable number of tropical varieties have been classified under the general category of "Tropical Flints." For the present we are restricting the term Guatemalan Tropical Flints to a fairly homogeneous race of which we have one collection from Mexico, several from Cuba, and a number from Guatemala, principally on the Caribbean side. The cobs are short to medium but proportionately broad and the seeds are small. The kernels are regular in size and shape and the rows are very straight and sulci evident though not very large. The tassel is much larger than in most North American varieties and there are more branches (the average number is over 20) but the rachises are more slender and the spikelets smaller. Condensed internodes are very rare as are also subsessile spikelets, and the tassel branches by comparison with those of most North American corn look more delicate and more regular.

The race is characteristically flint but slight indications of denting are frequently seen. A small cap of white or light yellow is characteristic and there is variation in color.

Guatemalan Big Grains (fig. 6; pl. 11 G, H, I).—

The outstanding characteristic of this race is the shape of the cob, which is large, sub-cylindrical with a more or less conspicuously enlarged base. The rows are usually straight in the cylindrical portion and too irregular to be recognizable in the enlarged portion. In color the race varies greatly, bright colors being the rule. The

Figs. 4–7. Ear and tassel characters for 5 races of maize: fig. 4, Mexican Pyramidal;
fig. 5, Guatemalan Tropical Flint; fig. 6, Guatemalan Big Grain; fig. 7, Racial averages
(GBG, Guatemalan Big Grain, PP, Pima-Papago, GTF, Guatemalan Tropical Flint,
MP, Mexican Pyramidal).

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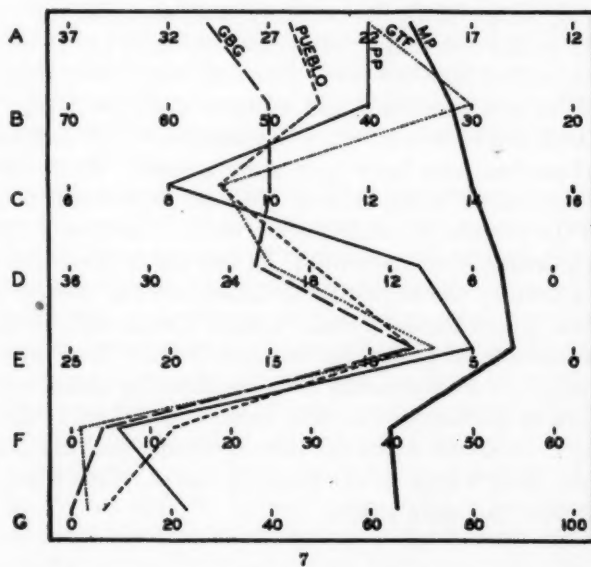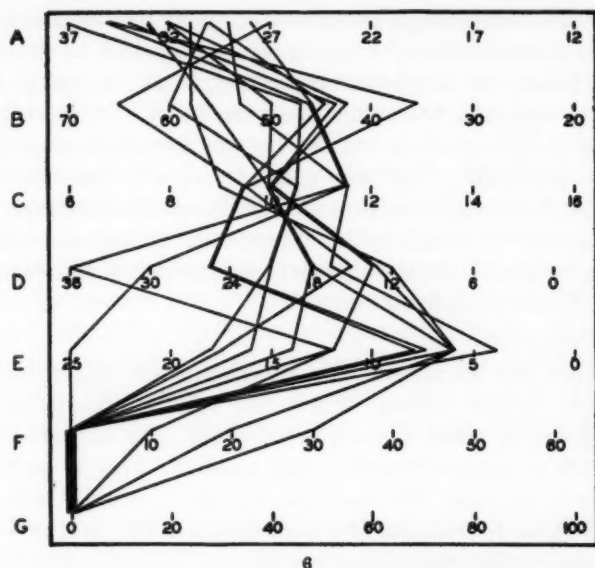
In figs. 4–6 each line represents an individual plant and shows its value for 7 different characters as follows: A, median cob width in cm.; B, kernel width × thickness in sq. mm.; C, kernel length in mm.; D, number of tassel branches; E, length of sterile zone in mm.; F, % greatly condensed internodes; G, % sub-sessile spikelets.

majority are flints though we have some flour varieties and a number of semi-dented flints. The tassels are similar to those of the Tropical Flints but are even larger and, in our material at least, were characterized by their lax drooping habit. They tend to have very long sterile zones at the base of the branches even up to 10 or 20 cm. in length. The only plant to show subsessile spikelets had already been suspected on ear characters of having been crossed with a Mexican Pyramidal. Condensed internodes are occasionally seen, but, on the whole, the tassels look very much like those of the Tropical Flints as defined above.

Pima-Papago.—

With very few exceptions these varieties are either white or a bright light yellow. Flour corn is the rule, though flints are occasionally found, while denting is unknown. The kernels are small but the cob is proportionately even smaller. This is particularly noticeable at the base. The ear tapers slightly, usually toward both ends, and there is evidence of compression in the narrow base and in lengthwise striations across the kernels. The inner husks are proportionately wide. While the rows are often straight, the individual seeds vary so much in shape that when looking at an ear one notices the kernels rather than the rows. For this reason they look more or less like tiles in a pavement and we have used the term "mosaic-seeded" to describe this effect. The tassels are stiff and harsh and though of medium size have very large glumes. While sub-sessile spikelets are not as common as in Mexican Pyramidal corn, about a tenth of the internodes usually show them. Condensed internodes also occur, though less frequently. As was stated above, these varieties are grown by the agricultural Indians of the deserts near the delta of the Colorado, the Pima, Papago, Yuma, etc. To archeologists this maize is of particular interest because it is very similar to the prehistoric Basketmaker corn which is the oldest recognized type of corn in the Southwest. The habit of the plant is distinctive. Compared to corn-belt dents the stem is slender and the internodes are long for their width, as are also the leaves. Tillers are usually sub-equal with the main stalk.

Pueblo.—

This race is very different from the above and is apparently allied to the Big Grains of Central America. It is characteristically big-cobbed and big-shanked. The ears are long and straight-rowed and the sulci are distinct. While the kernels are by no means so

wide as those of the Central American Big Grains, they are larger than the Pima-Papago and more regular. The base of the ear is usually square or sightly rounded though an enlarged base is occasionally seen. The kernel is either flour or flint and a very faint semi-dent is quite common. The kernel is usually colored, and most white varieties show obvious influence of Pima-Papago in other characters beside color. The tassel is larger than that of the Pima-Papago race with nearly twice as many tassel branches on an average but with slightly smaller glumes. Sub-sessile spikelets are rare but nearly every tassel shows irregular internodes and about one out of ten is obviously condensed. Some plants have a peculiar growth habit. The internodes tend to be short and the leaves wide. The tassels are not greatly exserted and the ears are long, giving the whole plant a curious "squatty" appearance.

SUMMARY

The need of a modern natural classification for the kinds of maize is discussed. Natural and artificial classifications are contrasted and illustrated by simple examples. It is pointed out that each has its advantages and disadvantages; artificial classifications are simple and comprehensive but do not integrate a large number of facts; natural classifications are often difficult to make and cumbersome to use but when they can be achieved they integrate the maximum number of facts.

The difficulties of grouping *Zea Mays* into natural races and subraces are discussed. For the purpose of this paper a race or subrace is defined as a number of varieties with enough characters in common to permit their recognition as a group; in genetical terms it is a group with a significant number of genes in common.

The external morphology of the corn plant is outlined with reference to those characters which might be used as criteria for the recognition and description of race, and the application of these criteria to the classification of maize is illustrated by examples. Indian varieties of maize from the Southwest belong to two main races, the Pueblo and the Pima-Papago, with a few recent admixtures and some obvious intermediates. The first of these races is grown chiefly by the Pueblo-dwelling Indians of the plateaus, the second by desert peoples near the delta of the Colorado River. The latter is very similar to the corn of the prehistoric Basketmakers.

Three Central American groups are described and illustrated,

though their exact relationships are as yet uncertain: (1) the Guatemalan Big Grains, (2) the Guatemalan Tropical Flints, and (3) the Mexican Pyramidals. The last is of particular interest because of its association with the territory of the Aztecs and its relation to modern corn-belt varieties.

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EXPLANATION OF PLATE

PLATE 11

Photographs of ears and tassels *(to different scales)* of representative plants of three races of maize, as follows: upper row, Mexican Pyramidal; middle row, Guatemalan Tropical Flint; bottom row, Guatemalan Big Grain. The ears were collected by Cutler at the points listed below, and the tassels are from seeds taken from the ears and grown at College Station, Texas, and Cienfuegos, Cuba. Except in one instance (E on the plate), the tassel associated with each ear was grown from seed taken from that particular ear. The ears have been somewhat mutilated in measuring mid-cob width. The scales in the center of the figure each represent 5 cm.; the scale to the left is for the ears, the one to the right for the tassels.

Figure	*Cutler's collection number*	*Source of ear*	*Number of ear from which tassel was grown*	*Place at which tassel was grown*
A	42	Xochimilco, Mex.	42	College Station
B	45	Xochimilco, Mex.	45	College Station
C	2	Toluca, Mex.	2	College Station
D	61	El Progreso, Guat.	18	College Station
E	18	Joyabaj, Guat.	18	Cienfuegos
F	24	Chicaj, Guat.	24	College Station
G	16	Coban, Guat.	16	College Station
H	5	Quiché, Guat.	5	College Station
I	6	Chimaltenango, Guat.	6	College Station

PLATE 11
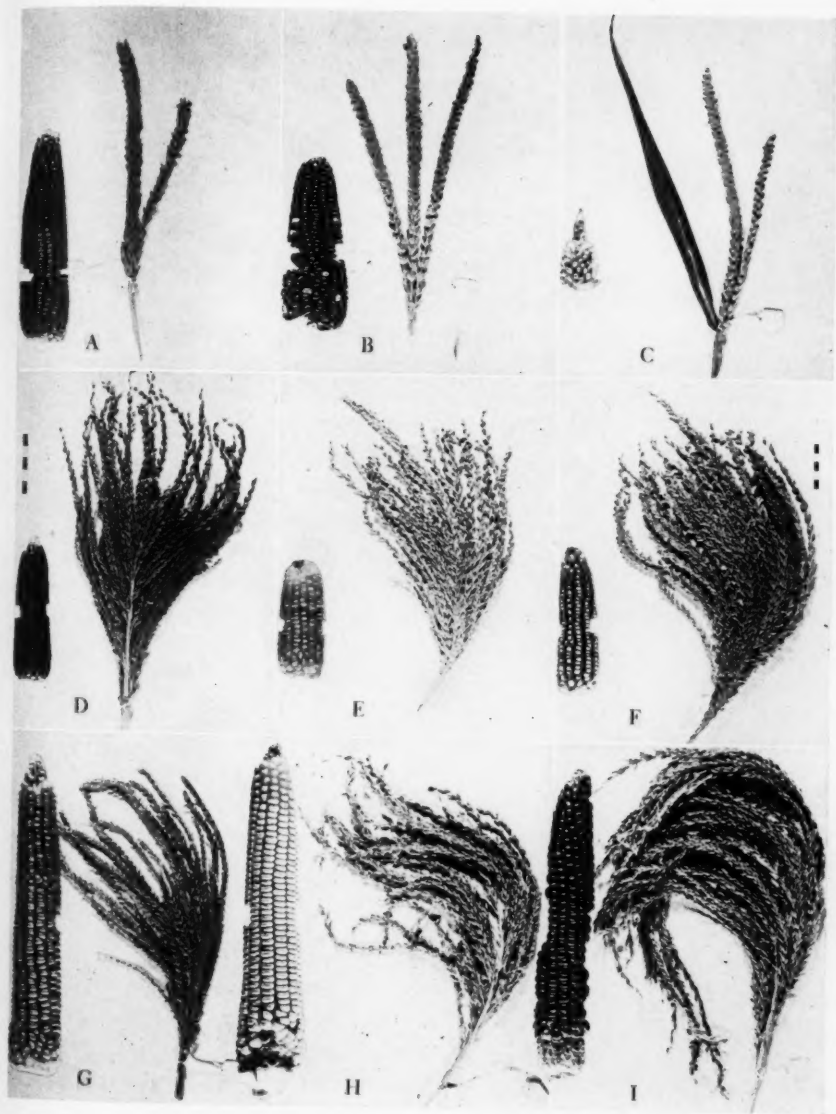
ANDERSON AND CUTLER—RACES OF ZEA MAYS

DOLOMITIC GLADES OF EAST-CENTRAL MISSOURI

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A characteristic feature of the landscape of the Ozarks is the occurrence on south- and west-facing hillsides of barrens which are locally known as "glades" or "cedar glades." Such glades, occurring on outcrops of thin-bedded dolomite or dolomitic limestone, principally of lower Ordovician age, have been studied in the area shown on the map (fig. 1). It includes about three-fourths of Jefferson County and small parts of adjacent Franklin, Washington and Ste. Genevieve Counties, Missouri, and lies from 25 to 50 miles west, southwest and south of the city of St. Louis, on the northeastern border of the Ozark Plateau.

The unique character of the Ozark glades has long been recognized by botanists, though no extended accounts have been published. Discussions may be found in the papers on the Ozark flora by Palmer ('21) and by Steyermark ('34; '40), who consider them as relics of the former plains flora of the region. References to the glades may also be found in the geological and geographical literature (e. g., Weller and St. Clair, '28; Pike, '28; Sauer, '20; Cozzens, '37; '39).

The present study is largely a by-product of two other investigations, by Brenner and by Erickson. Brenner's interest in the glades grew out of his study of the environmental variables at the Gray Summit Arboretum of the Missouri Botanical Garden (Brenner, '42). Erickson is engaged in a study of the distribution of *Clematis Fremontii* in Missouri, and the detailed mapping of the glades was done primarily as preliminary work for that study. Wraight became interested in the problem for its geographical and ecological implications. The analysis of the physical characteristics of the glades which follows is largely due to the field work of Brenner and Wraight.

This paper is primarily descriptive, but an attempt has also been made to analyze the factors which are responsible for the occur-

(89)

rence of the glades and for their characteristic physical conditions. Although a detailed treatment of the flora is beyond the scope of the present paper, the following remarks may be made. The glades are sometimes completely treeless, but more often there are "islands" of small trees surrounding gullies or ledges of rock. The species most frequently found are:[1] *Juniperus virginiana, Quercus Muhlenbergii, Q. stellata, Celtis pumila, C. pumila* var. *georgiana, Acer saccharum* var. *Schneckii, Rhamnus caroliniana, Vitis Lincecumii* var. *glauca, Cornus florida* and *Bumelia lanuginosa.*

Most characteristic of the glades, however, are the herbaceous species. A partial list includes: *Andropogon provincialis, A. scoparius, Panicum virgatum, Sporobolus heterolepis, Bouteloua curtipendula, Allium stellatum, Nothoscordum bivalve, Agave virginica, Arenaria patula, Clematis Fremontii, Draba cuneifolia, Leavenworthia uniflora, Baptisia vespertina, Psoralea esculenta, Petalostemum purpureum, Croton capitatus, Euphorbia corollata, Viola pedata, Oenothera missouriensis, Polytaenia Nuttallii, Asclepiodora viridis, Acerates viridiflora, Heliotropium tenellum, Scutellaria parvula, Houstonia angustifolia, Solidago Gattingeri, Aster oblongifolius, Silphium laciniatum, S. terebinthinaceum, Rudbeckia missouriensis, Echinacea pallida* and *Coreopsis lanceolata.*

Although the grass cover of the glades is rather sparse, usually consisting largely of separated clumps of *Andropogon*, the grass is the most conspicuous of the herbaceous plants (fig. 4). Despite the grassy appearance of the glades during most of the year, there are a number of other plants which, during their blooming periods, cover the glades with solid masses of flowers. Such plants include both annuals like *Leavenworthia uniflora*, which flowers in April, and perennials such as *Rudbeckia missouriensis*, which carpets the glades in late July and early August. The glade species are all more or less xerophytic, and a number of them are remarkable for their linear or finely divided leaves.

In mapping the glades, use was made of the aerial photographs on file at the offices of the county Agricultural Conservation Associations. The photographs were taken at an altitude of about 13,000 feet and are printed to a scale of 8 inches to a mile. Most of them

[1] The list of species given here agrees with Palmer and Steyermark's ('35) catalogue, although the authors realize that, in some instances, that work is not up-to-date in nomenclature.

DOLOMITIC
GLADES
IN
JEFFERSON COUNTY
MISSOURI
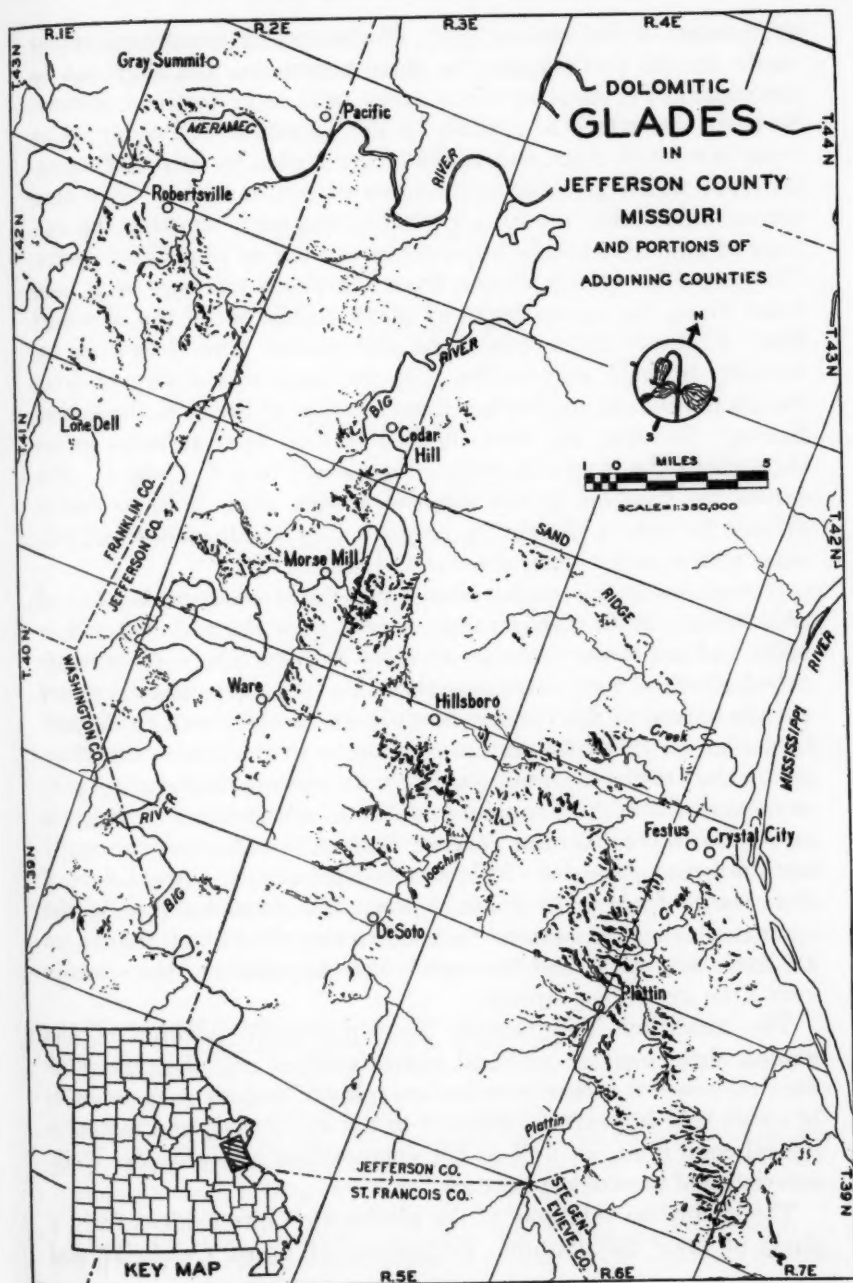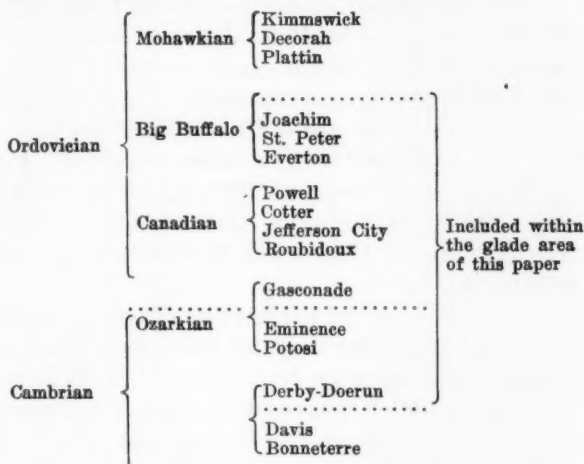AND PORTIONS OF
ADJOINING COUNTIES

FIGURE 1

were taken in September, 1937. Glades can be recognized rather
easily on the photographs by their whiteness, and they can be
distinguished from other white areas, such as bottomland pasture,
by their characteristic outline, by the islands of red cedar which
occur in most of them, and, in the larger glades, by ledges of resist-
ant rock which give the appearance of contour lines. For each
square mile within the area, a tracing was made showing the out-
lines of glades and some other features such as roads and creeks.
The map (fig. 1) was drawn from the photo tracings on a base
taken from the county highway maps published by the Missouri
State Highway Department. All the glades were drawn as ac-
curately to scale as possible. The drainage was drawn in from
the photo tracings and the topographic maps of the U. S. Geological
Survey. The map has been checked by field work to some extent
throughout the area and rather completely in a few places. The
errors are confined to the smallest glades, since it is somewhat
difficult to make a distinction between very small glades and hill-
sides with a rather open cover of red cedars.

The glades in this region almost invariably occur on south- and
west-facing slopes. They rarely extend over the top of a hill or
ridge and are never found in a valley bottom. The soil mantle is
extremely thin, very often less than one inch deep, and there are
always numerous flat fragments of the bed rock strewn on the sur-
face (fig. 4). The ground-water relations of the glades are char-
acteristic. During late autumn, winter and spring they are typically
so saturated that there is almost continual seepage, and such plants
as *Nostoc terrestris* and *Isoetes Butleri,* members of normally
aquatic genera, flourish. This saturation leads to a great deal of
disturbance from frost heavage when the ground thaws in the
spring. During the summer months, on the other hand, the glades
are extremely xeric, and for a period in the middle of the summer
very little green may appear.

The conditions determining the topographic position of the
glades, their unusual physical characteristics and their peculiar
flora represent a rather complex interplay of factors such as angle
of slope, thin soil mantle, attitude to the sun's rays, and meteoro-
logical conditions, as well as the composition and physical char-
acteristics of the underlying rock.

The geological relations of the glades are quite evident from a
study of their distribution. Formations of upper Cambrian and

middle and lower Ordovician age outcrop within the area of this study, the geological column being as follows:[2]

Ordovician	Mohawkian	Kimmswick / Decorah / Plattin	
	Big Buffalo	Joachim / St. Peter / Everton	Included within the glade area of this paper
	Canadian	Powell / Cotter / Jefferson City / Roubidoux	
Cambrian	Ozarkian	Gasconade / Eminence / Potosi	
		Derby-Doerun / Davis / Bonneterre	

These formations present some lithologic contrasts, including a variety of sandstones, limestones, shales and dolomites. The dolomites are of particular importance, since the presence of thin-bedded, relatively non-cherty dolomite (fig. 5) appears to be the decisive factor in the production of glades. The largest glades occur on the outcrop belt of the lower part of the Powell formation, which includes the greatest thickness of such rock in the column. Similar dolomitic strata are found in the Joachim formation, the upper portion of the Everton, the Cotter, the Jefferson City and perhaps in all the other formations listed above except the St. Peter sandstone, the Roubidoux formation and those formations above the Joachim. The largest and most numerous glades, as stated above, occur on outcrops of the lower Powell.[3] The Cotter and Jef-

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[2] The geological column is reproduced from the Geological Map of Missouri, with the omission of formations absent from the area of this study.

[3] The formations of the Canadian Series are notoriously difficult to distinguish in the field. They vary greatly in lithology within short distances, both vertically and horizontally, and fossils are difficult to find. The geological correlations of the glades made in this paper are based upon the geological map accompanying Pike's ('28) dissertation on the Crystal City quadrangle, which agrees in interpretation with the map of Ste. Genevieve County of Weller and St. Clair ('28); on personal conversation with Mr. James S. Cullison; and on such field identification by the authors as was possible.

Cozzens ('37; '39) has correlated the glades with the Cotter formation. While the Powell is the most important glade-producer in the southern part of the area described

ferson City, which, with the Powell, constitute the Jefferson City group of the state geological map, are next in importance as glade-producing formations. Small glades are found frequently on the Joachim; the location of the St. Peter-Joachim escarpment (Sand Ridge) is indicated in fig. 1 by the glades on this formation. The Everton is of slight importance in this study. The Gasconade, Eminence and Potosi formations are not important, but small glades apparently occur occasionally. The numerous small glades in northeastern Washington County (T.39N, R.3E) are found on the Derby-Doerun. Glades are reported to occur on the Bonneterre formation (Sauer, '28, pl. III a), but its outcrop lies outside of the area investigated.

In the area of the Plattin and Kimmswick outcrops, south-facing slopes have a sparse tree cover in which red cedars often predominate, and in some places there are few, if any, trees. However, such slopes in the Plattin and Kimmswick country are much steeper than in the area of this study, and there is no thin-bedded dolomite. Where the hillsides are barren enough to justify the term glade, the appearance is quite different both floristically and lithologically from the dolomitic glades. Glades occur on the St. Peter sandstone which also support a different flora from that of the dolomitic glades.

Besides the lithologic character of the rocks, a second factor determining the areal distribution of glades is the amount of local relief. The glades lie almost wholly within the Mississippi and Missouri River Border Provinces defined by Sauer ('20, fig. 18), which are equivalent to the River Border Region of Cozzens ('39, fig. 4). The region as a whole is one of moderate relief for the Ozarks, values of 300 to 400 feet being given by Cozzens, but there is, of course, considerable variation within the region. Glades seem to occur only where the proper lithologic conditions are found in conjunction with relatively high local relief. For instance, reference to the map will show that there are practically no glades between Hillsboro and Sand Ridge. This area is underlain by the same thin-bedded dolomite which elsewhere produces glades, but the relief is not sufficient to allow their development here. In the southeastern part of T.40N, R.5E, one to three miles north of the

here, the only part for which a large-scale geological map is available, the glades are by no means limited to the Powell. Considering the variability of the Jefferson City group from place to place, the Cotter formation may very well be the most important glade-former elsewhere.

Fig. 2. Glade on lower part of the Powell formation, one mile north of Plattin (SE ¼, S. 36, T. 40N, R. 5E). All the photographs were taken in January, 1942.

Fig. 3. Severely grazed glade, 2½ miles southeast of Hillsboro (NE ¼, S. 14, T. 40N, R. 4E).

Fig. 4. Portion of the glade shown in fig. 2.

Fig. 5. Recent road cut near Hillsboro, showing thin-bedded dolomite of the kind on which glades occur.

village of Plattin, on the other hand, where rock of the same lithology underlies land dissected by tributaries of Plattin Creek, glades occur on every ridge.

Much of the rock scattered on the surface of the glades is soft and friable, and is called "cotton rock" by residents of the Ozarks. Samples from several localities were tested for dolomite content by the method described by Brenner ('42, p. 104), with results indicating a very high proportion of dolomite crystals. Porosity tests showed about 25 per cent pore space, as compared with values of 3 to 9 per cent for massive dolomite and limestone from the same localities, and 10 to 12 per cent for sandstone.

Soil tests made on the glades at Gray Summit (S.17, T.43N, R.2E) indicated a slight acid reaction and a high organic content. There is very little material corresponding to the leaf litter of the adjacent woods, and the high organic content should probably be ascribed to slow decomposition rather than abundant supply of organic material. This is related to the meager soil flora and fauna, which is in turn due to the extreme variations in temperature and moisture conditions of the glades. It is probable that the amount of available plant nutrients in the glade soil is low, though no attempt has been made to investigate this point.

Probably more important than the chemical composition of either the rock or the soil is the thin-bedding of the dolomite (fig. 5). The beds vary from a fraction to three or four inches in thickness, and contain numerous vertical joints. The presence of bedding planes and joints, along with the extreme porosity of some of the beds, results in ample space for subsurface water. The thin-bedded strata which outcrop in the glades are typically underlain by relatively impermeable massive strata, usually dolomitic, which check the downward percolation of water. This water moves laterally along the numerous bedding planes and, since there is no soil mantle to diffuse it, there is abundant seepage at the outcrops from late autumn to early summer.

Pluvial conditions are also important in the saturation of the glades during the winter and their desiccation during the summer. The mean annual precipitation in this region is about 43 inches. On the whole, the greatest part of this falls during the summer, and the least during the three winter months. At Union, which can be taken as typical of the glade area, since it is only about three miles west of the area included in the map, there are two peaks of

4.54 inches in May and 4.70 in August, and a minimum of 2.20 inches for February. The effective precipitation for the glades, however, presents a somewhat different picture. During the winter and spring months, the rhythmic succession of cyclonic storms brings some sort of precipitation at least once a week. This is usually in the form of a slow drizzle resulting in relatively high infiltration and low run-off, hence much water passes underground. Furthermore, little water is lost by evaporation because of the relatively low temperature and high humidity during such periods of precipitation. This saturation may be an important factor in excluding species of the upland climax from the glades by encouraging winter rotting.

During the summer, on the other hand, precipitation is very irregular and in the form of violent, erratic thunderstorms, separated by longer or shorter periods of drought. During such storms the volume of water falling in a given period is great, runoff is excessive and infiltration is low, hence little water goes underground, particularly on the glades where the soil mantle is thin. The high temperature and low humidity which often follow such thunderstorms further reduce the effective precipitation. Again, the thin soil of the glades contributes to their xeric condition in the summer. A thick layer of soil normally forms a mulch which retards evaporation of subsurface water. The lack of such a mulch on the glades makes for rapid desiccation during warm weather.

The angle of slope of the glades is relatively steep and it appears to be an important factor in determining their characteristics. The slope of a few large glades has been measured by hand-leveling and pacing. There is considerable local variation in gradient at different levels, which can be ascribed to the presence of strata of different resistance, but the average slope appears to vary from 15 to 20 per cent, while that of adjacent north-facing wooded slopes approximates 10 per cent. This steep gradient permits even small volumes of water washing down the slope to carry a considerable load, and is probably one of the principal reasons for the thin soil cover. The steep slope of the glades, coupled with their southern and western attitude, gives them a high angle of incidence to the sun's rays during the warmest part of the day. The attitude of the glades also exposes them to the drying effect of the prevailingly southern winds of the Ozark region.

In the opinion of the writers the dolomitic glades of this area

are permanent ecological entities, entitled to be called an edaphic climax, rather than the first stage in the succession leading to a sugar maple-white oak climax, as they have been regarded by Steyermark ('40, p. 372 et seq.). The fact that open grassland was formerly much more extensive in the Ozarks, and that, with the white settlement of the country and the accompanying reduction of fires, there has been a widespread invasion of the grassland by forest, is too well documented to be doubted. However, the extensive Ozark grasslands of the early nineteenth century occupied hill and ridge tops, where glades rarely occur, and there is no reason for believing that they owed their existence to any more permanent factor than the annual fires which were encouraged by the Indians and early settlers. The dolomitic glades described here, however, seem to present too extreme a set of environmental factors to permit their invasion by trees of the upland climax of this region. The glades seem to be so largely determined by the character of the geological substrate that it would appear to require a rather large-scale change in climatic conditions to obliterate them.

Many of the glades are subjected to grazing by cattle, and to a lesser extent by hogs. Grazing naturally aggravates the barrenness, and occasionally the overgrazing is so severe that practically no plant cover remains. At best the glades produce poor pasture, and a considerable proportion shows no evidence of grazing. It does not seem probable, from a comparison of grazed and apparently ungrazed glades, that they owe their existence to grazing. On the contrary, moderate grazing seems to encourage the appearance of red cedars.

It has been pointed out above that glades occurring on the St. Peter sandstone and on the Plattin and Kimmswick formations differ considerably in character from the dolomitic glades. Barrens are also found on the La Motte sandstone, and in granitic, porphyritic, and highly cherty areas of the Ozarks (Steyermark, '40; Palmer, '10). None of these have been investigated by the present writers, but they should probably all be distinguished from the dolomitic glades of this study.

The glades of this area bear resemblances to the glades and bald knobs of the White River region of Missouri and Arkansas, and to the cedar glades of the Nashville Basin in Tennessee (Harper, '26; Freeman, '33). Relations may also be pointed out between the flora of the glades and that of the Great Plains. The shale barrens

of Virginia and West Virginia (Wherry, '30; Core, '40) appear to represent a similar geologically determined habitat, and they have some floristic similarities to the glades in this area.

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SUMMARY

This paper is a description and analysis of a characteristic type of Ozark vegetation, known locally as "glades," which occur on outcrops of thin-bedded dolomite. A brief enumeration of the flora and a detailed map of these glades for an area in east-central Missouri are presented.

The areal distribution of the glades is determined by geological factors and local relief. Their environmental characteristics, most important of which are winter saturation and summer desiccation, are ascribed to a complex of factors, including thin-bedding of the dolomite, thin soil mantle, steepness of slope, and attitude to the sun's rays.

The glades are regarded as an edaphic climax rather than as a stage in the succession to forest climax.

The relation of the glades to similar vegetational areas elsewhere is discussed.

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THE ENVIRONMENTAL VARIABLES OF THE MISSOURI BOTANICAL GARDEN WILDFLOWER RESERVATION AT GRAY SUMMIT[1]

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INTRODUCTION

Included in the 1,296-acre tract representing the Arboretum of the Missouri Botanical Garden is a parcel of land, roughly 300 acres in extent, which has been set aside to be developed as a wildflower reservation. Here the native trees, shrubs and herbs peculiar to the various natural habitats will be brought together where the public can readily become acquainted with them. Here also rare or otherwise uncommon indigenous wild plants will be held safe from extinction by the hands of the predatory tourist.

It is the purpose of this paper to present a preliminary survey of some of the more important factors conditioning the various environments represented in the Wildflower Reservation of the Missouri Botanical Garden in order that its development may be carried on in a systematic manner. It is hoped that this investigation, despite its strictly elementary nature, will indicate the more important factors to be studied specifically and critically at some future date. An attempt will be made also to correlate the extant arboreal vegetation with the various environmental factors in order to arrive at bases for interpreting the distribution of the native flora. In the course of this study the geology, physiography, soils, and climatology of the area were investigated and the alteration of the flora by the activities of man was reviewed.

For the purpose of this study an area was selected which embraced the various habitats characteristic of the reservation as a whole. The area chosen is bounded on the north by a service road commonly known as the Ridge Trail, on the south by a line connecting the face of the cliff terminating Cliff Ridge to the east with the ledge terminating Ledge Ridge to the west. A line drawn down the

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crest of Cliff Ridge forms the eastern boundary of the area. A similar line drawn down the crest of Ledge Ridge bounds the area to the west.

GEOLOGY

The area lies on the northern border of the region of dolomitic limestone rocks which compose the greater part of the northern Ozark plateau. The rocks belong to the Canadian Series of the Lower Ordovician Period.[2] Two formations are represented, the uppermost stratum of the Jefferson City formation, and the Cotter formation.

METHOD OF STUDY

The rugged land-form of the area and the numerous outcrops of the bed rock made the study and accurate mapping of these outcrops comparatively easy. The cliff terminating Cliff Ridge on the east side of the area offered an excellent exposure for studying the stratigraphy. The thickness of the formations and their different phases were accurately measured with tape and plumb line. The rocks outcropping in the ledge that terminates Ledge Ridge on the west and the numerous outcrops of bed rock on either side of the valley dividing the area provided a sufficient number of stations for correlating the areal geology on a topographic map. A transect line was established up the valley, and from this line shorter lateral lines, at right angles, were made to the various points where outcrops occurred. The relative elevations of the different outcrops were obtained by means of a Brunton compass which was also used to measure the angles of the various slopes. Distances were paced off.

Since the two formations represented on the area are essentially dolomitic in nature, the examination of the chemical properties of the rocks was limited to a determination of the percentage of the dolomite crystals in the various formations or in such phases of these as had an apparent bearing on the vegetation.[3]

Early in this investigation it seemed advisable to study the physical properties of the various rocks, particularly those of the glades.

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[2] Weller, Stuart, and Stuart St. Clair. Geology of Ste. Genevieve County, Missouri. Mo. Bur. Geol. and Mines, II, **22**: 30–31. 1928.

[3] By polishing a smooth surface on the rock, then staining it with Lemberg's solution or molar copper-nitrate solution $Cu(NO_3)_2$, the dolomite crystals were easily differentiated from the calcite and other calcareous minerals.

Perhaps in such features as porosity and permeability might lie the basic cause for the development of the unique glade flora. The relative porosities of the various rocks were determined by gravimetric methods, using a procedure outlined by Melcher.[4] The permeabilities of the rocks were tested by comparing the depths to which a dye would penetrate in a given period of time. This procedure, though simple and providing little quantitative data, did, however, show the relative extent to which the rocks were permeable to the infiltration of ground waters.

STRATIGRAPHY[5]

The Jefferson City Formation.—The Jefferson City formation forms the lowest rock outcrop of the strata exposed in the area (fig. 1). The uppermost seven feet of this formation are exposed at only two stations, one in the mouth of the valley, the second at the base of the east end of the ledge terminating Ledge Ridge. The fact that this is the lowest of the rocks outcropping on the area has caused it to be covered with talus debris over the greater part of its range. The rock is a dolomitic limestone, for the most part massive, oolitic, and light buff to gray-brown in color. It has a comparatively low porosity, approximately 5 per cent, is quite permeable, and contains 30 per cent of dolomite crystals. No unconformities are evidenced between the Jefferson City formation and the overlying Cotter formation.

The Cotter Formation.—The remaining rocks outcropping on the area belong to the Cotter formation. Unlike the underlying Jefferson City formation, deeply overlain with talus debris, it presents a great areal exposure of bare rock surface. It was suspected that these various outcroppings, because of their different physical and chemical natures, were apt to be of direct influence on the flora. The formation is composed of phases of sandstones and dolomitic limestones. The limestones appear in both massive and thin-bedded phases, the latter being essentially "cotton rock."

The basal phase of the Cotter formation is one of gray to gray-red sandstone 37 feet in thickness. This sandstone, like the final

[4] Melcher, A. F. Determination of pore space of oil and gas sands. Trans. Amer. Inst. Met. Eng. 65: 496–497. 1921.

[5] The geological correlations made in this paper are based on a well log which is on file at the offices of the Missouri Geological Survey.
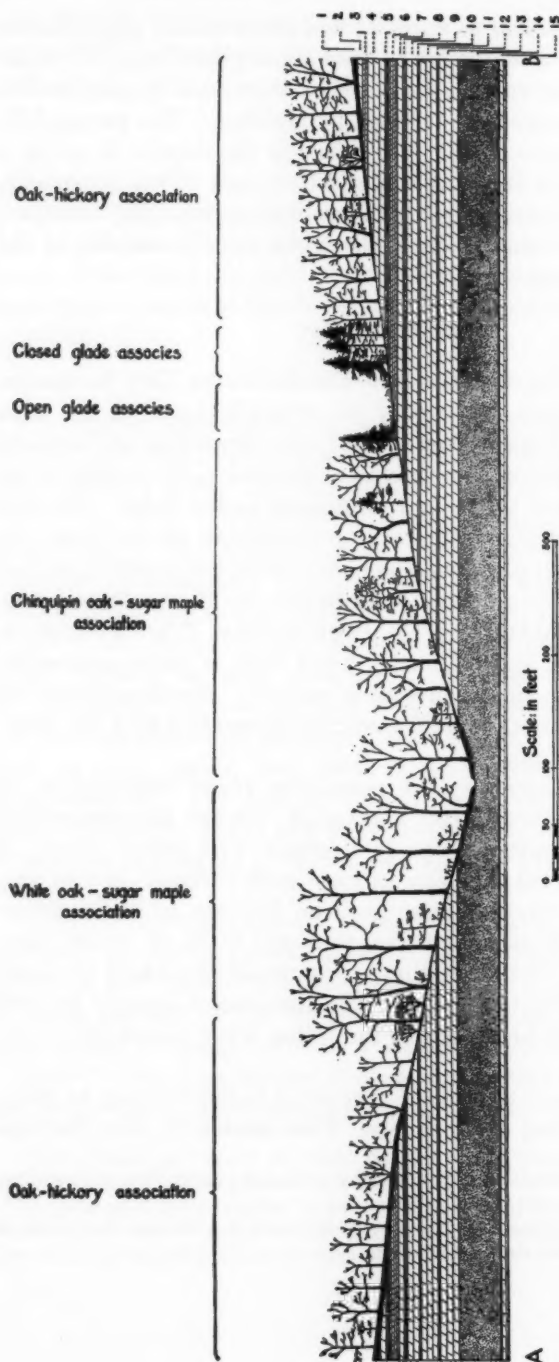
Oak-hickory association

Closed glade associes

Open glade associes

Chinquipin oak – sugar maple association

White oak – sugar maple association

Oak-hickory association

Scale in feet

Fig. 1.   Structure section through the area A–B (see fig. 2).

1. Soil—silt loam...Union silt loam
2-14...Cotter formation
   2. Limestone—massive, dolomitic; 3. "Cotton rock"; 4. Limestone—massive, dolo-
   mitic; 5. Sandstone—red; 6. "Cotton rock"; 7. Limestone—massive, dolomitic;
   8. "Cotton rock"; 9. Limestone—massive, dolomitic; 10. Sandstone—gray; 11. Lime-
   stone—massive, dolomitic; 12. Sandstone—gray; 13. Limestone—massive, dolomitic;
   14. Sandstone—gray
15. Limestone—massive, dolomitic..................................Jefferson City formation

phase of limestone of the Jefferson City formation which it over-
lies, is almost entirely covered with a mantle of talus, though num-
erous small outcrops occur on the valley slopes and in the bed of
the wash draining the valley. Overlying this sandstone phase is
one of massive limestone 34 feet in thickness and having an inter-
calation of sandstone about 2 feet thick near its center. Like the
higher massive dolomitic phases of the formation, it has a rela-
tively small proportion of pore spaces, 5 per cent, is quite highly
permeable, and contains 40 to 50 per cent of dolomite crystals.
Chert nodules and lenses, white, brown, to pinkish-blue in color,
commonly occur. This phase outcrops in entirety on the face of
the cliff at Cliff Ridge, forming a series of high step-like ledges.
On the valley walls it has been smoothed off by erosive agents and
is overlain by a mantle of chert and float material from strata above.
A fine-grained, gray sandstone overlies this massive phase to a
depth of two feet and this in turn is overlain by a phase of massive
dolomite $9\frac{1}{2}$ feet thick and having a six inch phase of sandstone
intercalated four feet above its base. Three feet of thin-bedded
dolomite, ''cotton rock,'' overlie this massive phase and in turn
are overlain by another five feet of similarly massive dolomite and
seven feet of thin-bedded dolomite. The last is typical ''cotton
rock,'' pink or buff to gray in color, easily fractured, and in beds
from $\frac{1}{2}$ to 4 inches thick. Exhibiting the highest degree of porosity,
24 per cent, of all the rocks occurring on the area, and composed
of pure dolomite, $CaMg(CO_3)_2$, together with a very high degree of
permeability, it is indeed a most interesting rock. The thin beds are
intercalated with very thin lenses of sandstone and a blue-white or
pink chert. Rarely, minute intercalations of shale occur between
thin beds of slightly argillaceous ''cotton rock.''

The small remaining portion of the formation has, for the most
part, been covered by the Union silt loam which caps the ridges.
Outcrops of these higher and final rocks of the formation are not
abundant within the area. A few occur at the head of the valley,
and some have been laid bare in the construction of the trail on the
crest of Cliff Ridge. The latter are thin-bedded, coarse-grained
dolomite with thin lenses and nodules of chert. A phase of putty-
gray shale six inches in thickness overlies the ''cotton rock'' and
is overlain by a medium-grained, loosely cemented, gray or red-
brown sandstone one to three feet in thickness. A five-foot phase
of massive faintly oolitic dolomite overlies the sandstone.

TOPOGRAPHY AND RELIEF

The area, essentially rugged, is in the mature stage of the erosional cycle, a feature typical of the hills and ridges bordering the southern face of the area to the north of the Meramec River.[6] Two ridges, Cliff Ridge and Ledge Ridge, truncated by an ancient meander of the Meramec River, rise 140 feet above the flood plain of that river (fig. 2). The cliff terminating Cliff Ridge, together
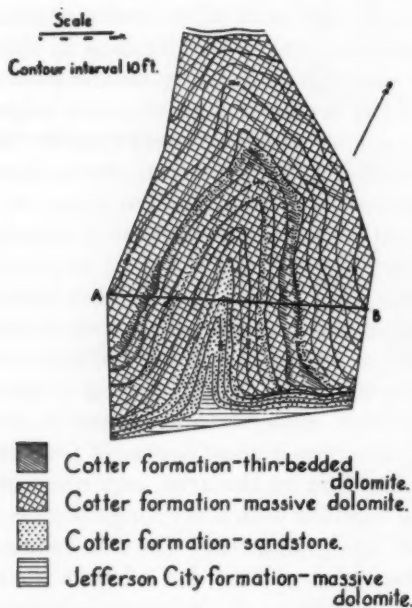

Scale

Contour interval 10 ft.

■ Cotter formation-thin-bedded dolomite.
▨ Cotter formation-massive dolomite.
▨ Cotter formation-sandstone.
▤ Jefferson City formation-massive dolomite.

a. □ Pastured 1890-1925.
b. ▨ Pastured 1890-1925; cut-over 1935
c. ▨ Pastured 1890?-1925; deforested 1900.
d. ▨ Deforested 1880; cultivated ?-?; pastured 1900-1925.

Fig. 2. Geologic map. A–B, location of geologic structure section.
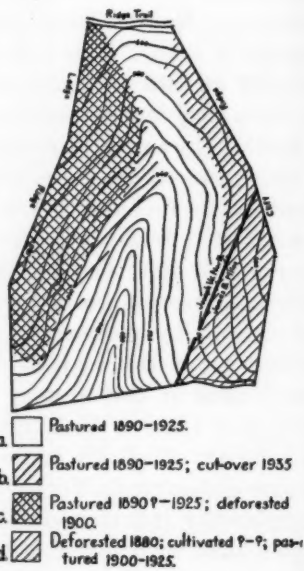
Fig. 3. Showing land use of the area 1880–1935.

with the high ledge facing truncated Ledge Ridge, and the numerous ledges, shelves and other outcrops enhance this rugged nature. A deep valley with a youthful "V" profile bisects the area (fig. 1). During the rainier seasons of the year a rivulet occupies the acute trough of the valley, carrying the waters drained from the adjacent uplands to the flood-plain where they are soon lost in the gravels underlying the silt. The ridges are, for the most part, narrow and appear as lateral spurs from the higher ridge serving locally as the

[6] Marbut, C. F. Soil reconnaissance of the Ozark region of Missouri and Arkansas. U. S. Dept. Agr., Bur. Soils and Field Operations, Rept. 13: 1727–1873. 1911.

drainage divide between Brush Creek to the north and Meramec River.

The area, as a whole, offered an interesting study in angles of slope[7] resulting from differential weathering of the formations and their included phases. A profile of the valley, taken at points A-B (figs. 1 and 2), shows the massive limestone of the Jefferson City formation overlain by the weaker, basal sandstone phase of the Cotter formation and this in turn by the resistant massive limestone. Here the angle of slope is quite high, 15 to 18 degrees, and few outcrops occur since the rock is deeply overlain by soils creeping down from above. This steep angle of slope persists through the massive phases of the Cotter formation where it is broken by the thin-bedded phase of that formation. Here the slope is about 10 degrees. The steeper angle is resumed by the recurrence of the second massive phase of the Cotter, represented in part by a low ledge. The second, thicker of the thin-bedded phases of the Cotter formation causes a conspicuous break in the angle of slope. Here the weakly resistant, thin-bedded rocks have been rapidly beveled off, and the angle of slope is more gentle, 10 degrees. A low ledge marks the thin sandstone phase overlying the "cotton rock," after which an even lower angle of slope, 5 degrees, is assumed and retained to the crest of the ridge.

SOIL SURVEY

The soils of the area have been classified by the United States Department of Agriculture, Bureau of Soils, as belonging to the sandy subsoil phase of the Union silt loam.[8] The report did not consider the smaller, more specialized types of soil, particularly those classified as "rough stony land." Such soils lie on the steep slopes of the ridges immediately north of the Meramec River in the vicinity of Gray Summit. Since a great portion of the area under investigation is covered by such soil, it was found necessary to study its physical and chemical properties to aid in the interpretation of the flora.

METHOD OF STUDY

Samples, weighing about 100 grams, of the upper six inches of the soil were systematically taken at 100-foot intervals across the val-

[7] Cozzens, Arthur B. Analyzing and mapping natural landscape factors of the Ozark province. Acad. Sci. St. Louis Trans. 30: 37–63. 1939.

[8] Vanatta, E. S., and H. G. Lewis. Soil survey of Franklin County, Missouri. U. S. Dept. Agr., Bur. Soils and Field Operations, Rept. 13: 1603–1633. 1911.

ley and at 200-foot intervals up the valley. After drying thoroughly in the air they were examined for content of organic matter, relative proportions of different sizes of soil particles, as recognized by the Bureau of Soils, and soil reaction or degree of acidity.

Analysis of Organic Content.—Ten-gram portions of the samples were taken along line A–B (fig. 2). After being weighed, they were heated in a crucible for 30 minutes over a hot Bunsen burner. They were weighed again after cooling, and any loss of weight was considered to be organic material removed by combustion. The results of these operations appear in TABLE I.

TABLE I

MECHANICAL AND ORGANIC-CONTENT ANALYSIS OF THE SOIL ALONG BELT TRANSECT B (see fig. 11)

Sample	% Rock & gravel	% Fine gravel	% Coarse sand	% Medium sand	% Fine sand	% Very fine sand	% Silt & clay	% Organic matter
1	0	0	.73	2.84	4.39	1.99	80.41	9.5
2	7.83	2.85	2.27	3.17	4.37	3.65	64.58	10.8
3	15.62	7.20	3.34	4.81	5.40	6.39	54.06	1.7
4 Glade	59.87	1.91	1.16	2.08	3.41	2.41	43.31	17.0
5	35.57	6.94	2.20	7.13	10.16	4.39	16.94	15.3
6	34.30	1.57	1.27	2.46	6.34	5.87	15.77	31.4
7	39.24	2.16	3.80	2.72	7.41	5.04	19.22	19.9
8	14.85	4.61	4.62	5.99	6.08	5.31	43.85	14.3
9	0	.179	1.61	4.58	4.58	5.024	73.71	10.1
10	0	.93	1.58	3.26	4.37	3.25	79.05	7.0
11	0	0	.85	3.07	4.32	3.36	84.56	3.9

Mechanical Analysis.—An analysis was made of samples taken along line A–B (fig. 2) to show the percentages of the different sizes of soil particles. Fifty-gram portions of the air-dried samples were weighed out. They were then dispersed in a mortar by gently rubbing with a pestle, after which they were shaken successively through a series of screens recommended for mechanical analysis of soils.

Soil Reaction (degree of acidity).—The samples taken over the whole area were tested for soil reaction with Brom Cresol Green,

Brom Cresol Purple, and Phenol Red indicators in a method described by Moore.[9] The results are compiled in fig. 6.

Soil Horizons.—Several test pits were dug at stations covered with a typical flora and suggesting a typical soil type. Where possible the pits were dug down to bed rock, but when the soil mantle was so deep as to make this impractical the approximate depth of the soil was tested by probing into the bottom of the pit with a crowbar. The thicknesses of the various soil horizons were measured and their color, texture, consistence, structure and porosity noted

a. Union silt loam, sandy subsoil phase, Main Ridge
b. Union silt loam, sandy subsoil phase, Ledge Ridge
c. Rough stony land, lower slope of Ledge Ridge.
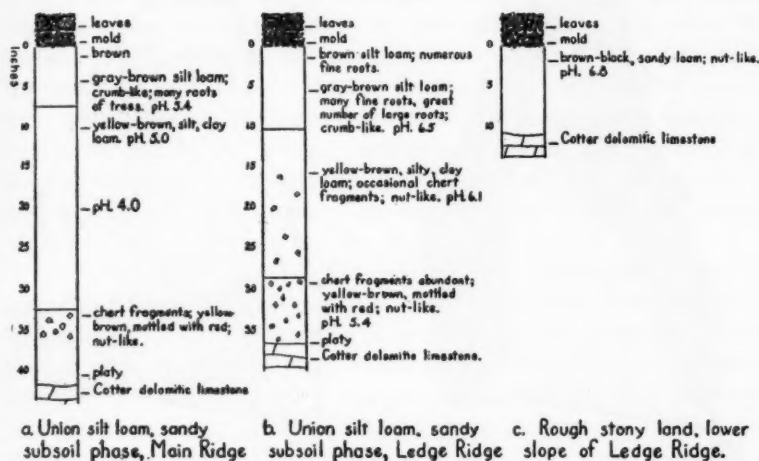
Fig. 4.   Soil profiles.

in accordance with recommendations made by Kellogg.[10] Sample profiles of the typical soils are shown drawn to scale in fig. 4.

THE SOILS

As was previously stated, the soils of the area have been classified by the Bureau of Soils into two distinct groups: the sandy-subsoil phase of the Union silt loam, and the "rough stony land."

The Union Silt Loam, Sandy Subsoil Phase.—The Union silt loam, sandy subsoil phase, is a brown or grayish-brown mellow silt loam 6–8 inches deep, which changes at depths between 8 and 20 inches into a light brown or yellowish-brown friable silt loam or

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[9] Moore, W. An improved method for the determination of the soil reaction. Brit. Golf Unions Jour. **4:** 136–138. 1935.

[10] Kellogg, Charles E. Soil survey manual. U. S. Dept. Agr. Misc. Publ. 274. 1937.

a silty clay loam. In structure the soil is crumb-like, grading into a nut-like subsoil (fig. 4a & b). Its origin is not perfectly understood, but its uniform nature over broad areas seems to suggest that it is loessial. An interesting character of this soil is the high proportion of fine sand grains (TABLE I). This soil lies as a cap, about 3–3½ feet deep, upon the crests of the ridges. Its loose sandy nature, together with the relatively high angles at which it lies on the slopes, has made it an easy prey to agents of erosion. In places

Union silt loam, sandy subsoil phase

Rough stony land

Rough stony land, glade phase)

Fig. 5.   Soil map.

pH. 4.0–5.4 – very acid.

pH. 5.5–7.0 – moderately acid–neutral

pH. 7.1 7.5 – moderately alkaline
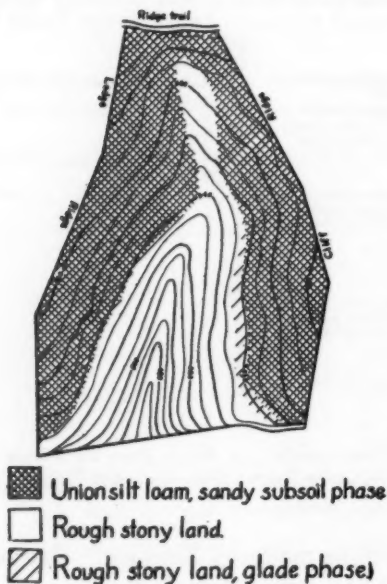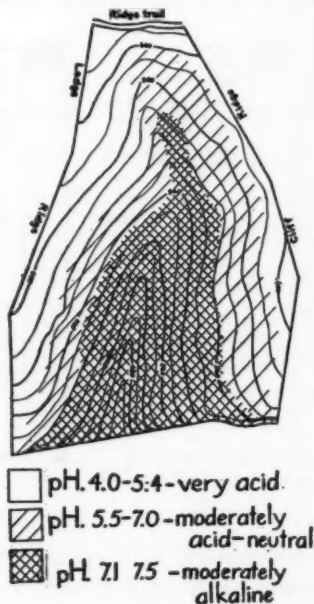
Fig. 6.   Showing distribution of different acid-alkaline soil types.

where the plant cover is sparse, as on the east slope of Ledge Ridge, many deep gullies have been eroded into the soil and subsoil horizons.

This soil, when treated with indicators, is found to be consistently very acid, from pH 4.0 to pH 5.4, the degree of acidity increasing as one proceeds to the lower soil horizons (fig. 4a & b). The low pH is perhaps partly due to its sandy, porous nature which has facilitated leaching to a moderate degree. There is also a decided tendency for vegetable litter to collect on the forest floor. It is in those places where the litter has collected to a considerable depth and

where it is predominantly of oaks and hickories, which is relatively slow to decay, that the lowest pH ranges are reached.

The soil shows a low content of organic matter, 1.7 to 10.8 per cent (TABLE I). The majority of the trees are of tap-root nature. Fibrous roots would tend to increase the organic content of the soil, but few such root systems are formed and they are necessarily short-lived. For the most part, few herbs are found on the forest floor on the ridges, and such plants are an important source of humus. Perhaps the poor herbaceous flora may be due to the thick layer of forest litter which prevents seeds and other propagules from reaching a suitable growth medium, particularly since the surface of this litter is dry for the greater part of the time. Also the forest floor is densely shaded during most of the growing season. Animal action in this soil is not particularly great. Comparatively few "signs," castings, burrows, or actual specimens of the more common subterranean animals were found in the course of sampling. The high degree of acidity and the low organic content of the soil might account for the poor fauna.

"Rough Stony Land."—The soil of the "rough stony land" is essentially residual and very shallow, from a mere film to 12 or 14 inches in depth. It is a very dark, brown-black to black sandy loam, plastic when wet, very brittle when dry, and essentially nut-like in structure (fig. 4c). The very shallow depth of the soil has permitted it to mature relatively early, which is indicated by the lack of definite horizons and the abundance of small insoluble fragments of chert. This soil may be considered as a vertically uniform mass. It contains a relatively high per cent of fine sand grains which increase as one progresses towards the valley (TABLE I). It is interesting to note the abundance of oolite composing these sand grains, a feature offering good evidence of the residual origin of this soil, for they have weathered out of the underlying oolitic dolomite rock strata.

This soil differs markedly from the Union silt loam of the ridges in being essentially a basic or lime soil. Soil tests show a pH range from very slightly acid, 6.8 at the uppermost limit, to alkaline, 7.5, in the valley (fig. 6). This soil contains a large amount of organic matter, 14.3 to 31.4 per cent, which increases steadily as one progresses down the slope and reaches its maximum in the valley (TABLE I). The high organic content of this soil, its shallow depth, and the massiveness of several of the underlying rock formations or their phases cause it to be exploited to a high degree by the roots

of trees and herbs. The high organic content makes this soil a valuable reservoir of infiltrated water and as a consequence able to support a rich herbaceous and arborescent flora. Animals are quite active here, numerous burrows, castings, puppae and specimens being noted.

"Rough Stony Land," Glade Phase.—This soil is limited to the glade, formed by the thin-bedded phase of the Cotter formation, on the west slope of Cliff Ridge (fig. 1). It is a very thin (from a mere film to 4 inches in depth) gray-brown silt loam. Soil reaction tests show it to have a pH range from 6.8 to 7.1, an essentially neutral reaction. An interesting feature of the glade soil is its high humus content, approximately 17 per cent. This can easily be understood when one remembers that the glades are of a xeric nature and therefore unfavorable to conditions of decay. The shallow depth of the glade soil and the generally xeric conditions tend too to discourage occupancy by subterranean animals, also important agents in the reduction of organic material.

CLIMATOLOGY OF THE AREA

The geomatic position of the area, between longitudes 90° and 91° West, and latitudes 38° and 39° North, places it in the temperate zone. Here the weather is governed by cyclonic conditions in winter. Local continental thunder-storms prevail in summer. The region has an annual rainfall of approximately 39 inches. The mean annual temperature is approximately 55° F. The last killing frost in the spring usually occurs about April 16, and the first killing frost in the autumn about October 22.

Accurate records of the precipitation on the area were not kept. However, a weather station at Pacific, Missouri, seven miles away, offers data which may be applied with reasonable reliability.[11]

Relatively accurate temperature records were kept on the area continuously for one year, at stations selected for extremes in environment. Thermometers were housed in specially designed shelters three feet above the ground. Comparisons were made of temperatures recorded on the ridge (Sta. A-1) and in the valley (Sta. A-2); on a west-facing slope (Sta. B-1) and an east-facing slope (Sta. B-2); on the open glade (Sta. C-1) and closed glade (Sta. C-2) (figs. 8–10). Temperatures of two-week periods were selected as representative of each season of the year. Unfortu-

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[11] Climatological data, Missouri section. U. S. Dept. Agr., Weather Bureau. 1940–1941.

nately, with only two recording thermometers available, continuous records at any one station were not possible, and in order to obtain a recording representative of each season the instruments had to be moved to another station every third week. This fact has prevented the direct comparison of most of the stations at a given time.

Comparison of Temperatures on Ridge (Sta. A-1) and in Valley (Sta. A-2).—In spring the ridge tends to be cooler during the day-
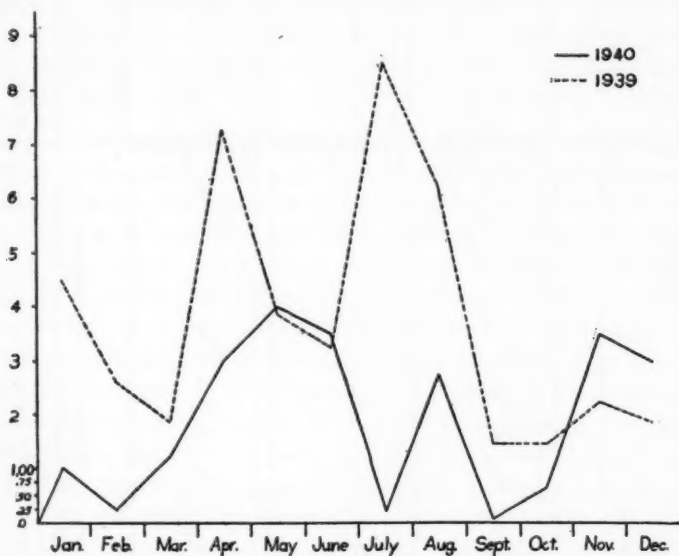

Fig. 7. Showing monthly precipitation in inches, at Pacific, Missouri, during 1939 and 1940.

light hours and warmer at night (fig. 8B). The valley tends to be from 2 to 5° warmer between the hours of 10 a. m. and 2 p. m., and about 1–7° cooler from 6 p. m. to 6 a. m.

In summer the ridge is consistently warmer than the valley (fig. 8C); in the night and very early morning, from 11 p. m. to about 6 a. m., it is usually only 2–4° warmer. For the remainder of the day, the ridge is about 5–8° warmer than the valley, except from 11 a. m. until 2 p. m., when it is only slightly warmer, 0 to 4°. The maximum mid-day temperature occurs at noon in the valley, due perhaps to the fact that after the sun drops several degrees past a vertical position the valley is again shaded by the foliage of the trees. The maximum mid-day temperature occurs at about 2 p. m.
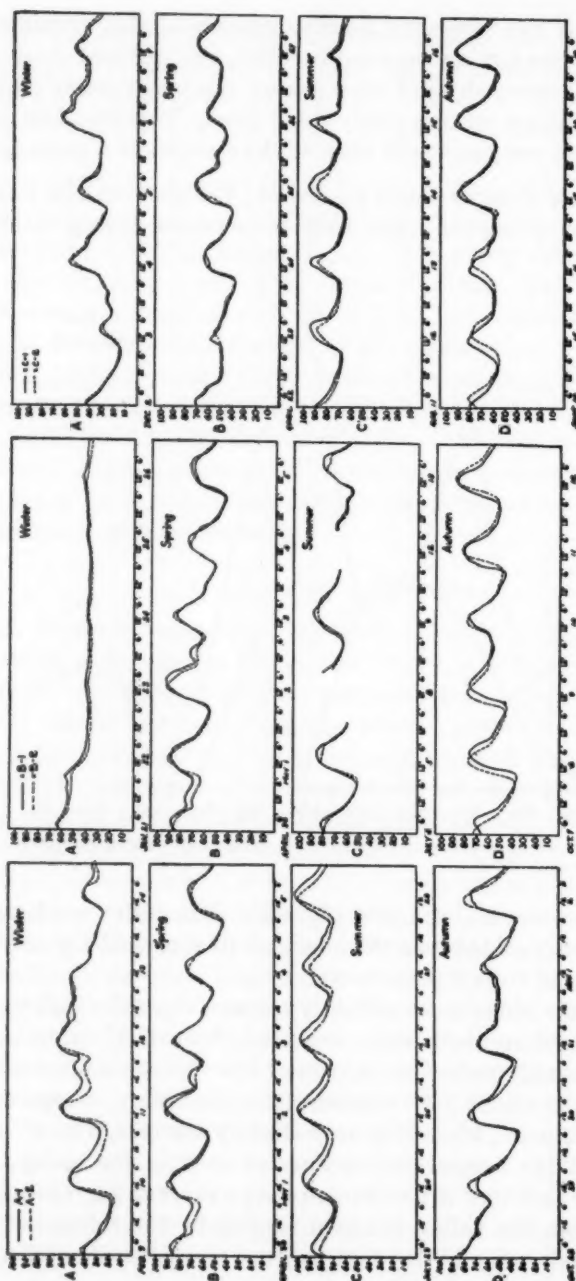
Fig. 8. Graphs of temperatures recorded as samples of seasonal variations between stations A-1 (ridge) and A-2 (valley).

Fig. 9. Graphs of temperatures recorded as samples of seasonal variations between Stations B-1 (west-facing slope) and B-2 (east-facing slope).

Fig. 10. Graphs of temperatures recorded as samples of variations between stations C-1 (open glade) and C-2 (closed glade).

on the ridge, where even after the sun has fallen from its vertical position it still penetrates through the less dense foliage.

With the approach of autumn and winter, the gradual loss of leaves by the trees permits a proportionately greater penetration of the sun's rays into the woods. It was noticed then that the maximum mid-day temperature in the valley was reached at noon as it was in the spring (fig. 8A and D). Similiarly, as the day temperatures in the valley increased, the night temperatures decreased. This marked difference in nocturnal temperatures is caused by the cooler, denser night air settling in the valley, a phenomenon known as air drainage. Day temperatures here tend to be 5–9° higher than those on the ridge, while night temperatures are 2–4° lower.

Comparison of Temperatures on West-facing Slope (Sta. B-1) and East-facing Slope (Sta. B-2).—In the early spring, autumn, and winter, when the trees are bare, the west-facing slope is strikingly cooler in the morning and very early afternoon, from 6 a. m. to 1 p. m. (fig. 9A, B, D). At this time the west slope was from 2 to 10° cooler than the east slope. During the late afternoon, evening and night the west slope is 2–6° warmer than the east slope. The maximum temperature of the day occurs at about 4 p. m. This rather odd distribution of temperature is caused by the attitude of the western slope to the rays of the sun. Exposed as it is, it is shaded in the morning and it is not until late afternoon that the rays of the sun strike it at a high angle and raise the temperature to the maximum point. At night this slope is somewhat warmer than the east-facing slope. This is because the sparse vegetation, the relatively large amount of exposed rock, and thin covering of mold and forest debris on the west-facing slope permit a great degree of heat radiation at night.

During late spring and summer the west-facing slope is consistently warmer than the east-facing one (fig. 9B and C). In general, the difference is small, only 1–4°, this being due to the relatively greater amount of heat-consuming moisture transpired by the more dense vegetation on the east-facing slope. As in winter, spring, and autumn the maximum day temperatures occur at about 11 a. m. on the east slope and at about 4 p. m. on the west slope.

Comparison of Temperatures on Open Glade (Sta. C-1) and Closed Glade (Sta. C-2).—In winter, early spring, and autumn the open glade is usually 3–8° warmer during the day than the closed glade (fig. 10A, B, D), an obvious condition when one remembers

the barren nature of the open glade. At night during these sea-
sons it is from 1 to 4° cooler than the closed glade where the con-
siderable abundance of junipers tends to make the air more quiet.
A denser covering of mold and litter on the forest floor prevents
rapid heat radiation which takes place on the barren open glade.

In summer, however, the open glade is constantly warmer than
the closed glade (fig. 10C), being from 3 to 8° warmer between
9 a. m. and 7 p. m. and usually 1–4° warmer during the night and
early morning. Normally it would be expected that the barren
nature of the open glade would favor rapid heat radiation and
that it would be cooler than the closed glade at night. However, a
canopy of broad-leaved trees cover the closed glade during the
growing season, which, together with numerous herbaceous plants
on the forest floor, create a more equable climate.

History of the Land Use of the Area

In order to interpret the relatively complex flora inhabiting the
area at present it was found necessary to learn the use of the land
from facts revealed by the area itself. The history was begun as
near as possible from the time when the land was first occupied by
the white settlers emigrating from the East up to its present use as
a wildflower reservation.

Use was made of data obtained from field notes taken on the area,
and of documentary evidence offered by an abstract to the title of
the land. Old trees were important sources of information concern-
ing the aspects of the original flora. The younger trees served as
indicators of changes in environment during the time that the area
has been occupied by white man. A survey and map of tree stumps
revealed the age of living trees of like diameter and also provided a
definite record of the former use of the land. The abstract to the
land title proved valuable by supplying the dates on which the par-
cels were granted to the first settlers. It also indicated the dates on
which the land fell into the hands of the various families and finally
the present institution, the Missouri Botanical Garden. The uses to
which the various portions of the area were put, together with the
time and intensity of use, were compiled in fig. 3.

The area is composed of two parcels of land which have had sep-
arate title histories up to the time that the Missouri Botanical Gar-
den acquired them (fig. 3). A small portion of the area, on Cliff
Ridge, represents part of an eighth section granted by the United

States to Edward J. Roberts on July 13, 1853. In 1881 it became the property of James B. Miles. The larger portion of the area is a part of the quarter section granted by the United States to William M. McPherson on June 19, 1851. Later the property was transferred to Powell; from Powell to Knapp in 1854; from Knapp to Crews in 1858; and from Crews to North in 1880. On March 12, 1925, both parcels of land were included in the area bought by the Missouri Botanical Garden.

An inspection of the area shows that it has been used in the following four ways, arranged progressively according to the degree to which the practice has altered the vegetation: (1) grazing, (2) light cutting over and grazing, (3) deforestation and grazing, (4) deforestation, cultivation, and grazing.

Grazing.—A survey of the area as a whole revealed it to have been generally and quite intensely grazed over. Though certain of the more ancient typical forest trees, oaks, hickories and maples, show decided preferences in their distribution, many younger specimens have a general distribution suggesting uniform conditions throughout the area. Such trees as red cedar *(Juniperus virginiana),* slippery elm *(Ulmus fulva)* and redbud *(Cercis canadensis)* are generally distributed and have been noted to invade local forested areas upon the advent of grazing.

Although it is evident that grazing is only one of the factors which have altered the vegetation of the area as a whole, there is a portion, representing slightly less than half the total expanse, on which grazing has been the only altering factor (fig. 3a). This fact is expressed by the total absence of stumps in a tract which contains an appreciable number of very old trees, obviously members of the virgin flora for their trunk diameters are comparable to stumps of trees calculated to be 175 to 260 years of age. These old trees have tall straight trunks and form a high canopy which, however, is broken in many places where individuals have died. Numerous dead specimens and standing "snags" are to be found, and many decaying trunks lie on the forest floor. Judging from the habit of the old trees, the aspect of the virgin forest was, for the most part, more closed and densely shaded. The present light open aspect of the forest suggests that a change of environment has taken place in a relatively short time. Throughout this plot there is a marked predominance of the group of trees referred to earlier in this account as indicative of intensive grazing. Counts of the annual growth

rings of red cedars are perhaps alone the best indicator of conditions accompanying grazing of local forest areas. Several counts were made on trees from different points of the plot, and 30–40 years was found to be the average age. Allowing 10–20 years for grazing to alter the habitat sufficiently to encourage invasion by the red cedar and other heliophilous trees, it becomes evident that grazing was begun here shortly after the land was acquired by Joseph North in 1880. Grazing was practiced over the whole area up to the time that it was bought by the Missouri Botanical Garden.

Light Cutting-over and Grazing.—A small portion of the area, that immediately bordering the old pasture on the east slope of Ledge Ridge and extending a short distance down the slope toward the ravine, was lightly cut over during the period that the Arboretum was maintained by government-supervised transient labor. These recently cut stumps have supplied data concerning the ages of the forest patriarchs, and have offered some idea as to the approximate ages of stumps and trees found elsewhere on the area. The removal of many old trees has produced a poor canopy of foliage and has made the forest here very open, almost park-like. The rich mold on the forest floor has proved to be an excellent seed bed, and a dense thicket-like growth of shrubs and saplings forms a lower stratum of vegetation. In addition to the older trees of the group which have invaded under grazing conditions, many seedlings of these species originated during the period following cutting-over and the resultant increased light on the forest floor (see fig. 3b).

Deforestation and Grazing.—Two portions of the area, which when combined represent approximately half of the whole, have obviously been deforested (fig. 3, c, d). Many stumps are to be found here, all of a uniform age and none from old trees. The cut-over portion represented on Cliff Ridge (fig. 3d) is divisible into two parts, each having been deforested at a different date. The portion representing the land formerly belonging to James Miles was apparently deforested about 60 years ago. Though no trees were cut to obtain counts of annual growth rings, comparison of the trunk diameters with those of other young trees of known age warrants this statement. The stump remains found here are in poorer state of preservation than those of more recently deforested portions, but the diameters of the stumps place the entire former vegetation in the class of virgin flora. When the approximate age of the trees was compared with the title to the land it was found that this por-

tion had been cut over about the time that the land was bought by James Miles.

The second, smaller portion of the deforested area on Cliff Ridge formerly belonged to Joseph North. The annual rings of several of the young trees now growing there were counted and showed the trees to be approximately 40 years old. The stumps, an undeterminable species of oak, found in this portion are in a better state of preservation than those of the trees cut from the Miles property. The age of the trees, together with the better state of preservation of the stumps, indicates this portion to have been more recently cut over than that on the Miles property, some 10–20 years after it was acquired by Joseph North.

It is evident that both portions have been grazed over quite intensely, for numerous islands of red cedar, slippery elm and redbud occur where the live stock succeeded in checking the rapid growth of the encroaching second growth of the forest.

Deforestation, Cultivation and Grazing.—A study of the plot on the east slope of Ledge Ridge (fig. 3c) has shown it to have been deforested and afterwards probably cultivated, for no stumps have been found there. Later on, and evidently for quite a period of time, it was apparently grazed and burned at intervals. A great number of the oaks and hickories now growing on the site exist as clumps composed of two to six trunks. This feature suggests that an old pasture already having a fair growth of seedling trees had been trampled by the hoof of livestock, or burned off, causing the original stem to die and numerous basal sprouts to spring up. The annual growth rings of several of these trees were counted and showed an average of 21. It is known that the site was still maintained as a pasture at the time of its purchase by the Missouri Botanical Garden in 1925. Relatively older trees, 40–60 years old, which border the plot on either side, have low limbs spreading into the clearing, indicating development as marginal trees. This fact places the clearing of this plot shortly after its purchase by Joseph North in 1880.

VEGETATION

The arborescent flora is a complex one composed of 28 genera and a total of 40 species. As noted previously, the large number of species and the relatively wide distribution of many of them over the area may, perhaps, be best attributed to human occupation rather than to natural causes.

METHOD OF STUDY

The complexity of the vegetation suggested that rather intensive methods should be applied to its study in order to secure a complete picture of the distribution of all the component genera and their species. A series of five 150-foot belt transects was run across the area at 150-foot intervals in order to obtain a complete and detailed map of the trees and shrubs. Because of the wide range of genera and species represented in the flora, and because of the presence among them of many small trees and shrubs considered as being valuable indicators of various abnormal conditions, practically no attempt was made to divide the flora into size classes on the basis of actual field measurements. However, record of the relative sizes of the various consistently large specimens was kept and is discussed below. Data obtained from these individual maps were arranged in graphical form. The survey of stumps used in the study of the land use of the area has also served in interpreting the relics of the virgin forest flora.

Belt Transects.—The transects were mapped by plotting, in linear fashion, a series of 50-foot quadrats across the area. Three such lines of quadrats were plotted adjacent to one another, thus forming a belt transect 150 feet in width across the area (fig. 11). Individual quadrats were marked with flagged staffs, oriented transverse to the area with a compass. Distances were paced off. The number of each species represented in the quadrat was counted in turn and noted in corresponding quadrats on individual maps. Figures 13–17 show species in each belt transect, together with their respective distributions across the area. Species having a similar distribution have been grouped together.

On the basis of the belt-transect maps and graphs showing the density of each species in the different belt transects, a composite map has been prepared showing the grouping of the species into associations and associes and their areal extent (fig. 12).

The terms, association, associes, and dominant, used in discussion of the vegetation in this study, have been used in the sense originally applied by Weaver and Clements.[12]

DISCUSSION

As stated above, the complex nature of the vegetation of the area is essentially a condition resultant of intensive grazing. Likewise,

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[12] Weaver, J. E., and F. E. Clements. Plant ecology, pp. 43–54. New York. 1939.

mention was made of a class of trees locally indicative of pastured
forest land. It seems essential at this point to review the succession
of conditions leading to the present state of the vegetation of the
area.

Judging from the habit of the various scattered ancient forest
trees, it is apparent that the aspect of the local forests before the
advent of man was, for the most part, open. The trees were widely
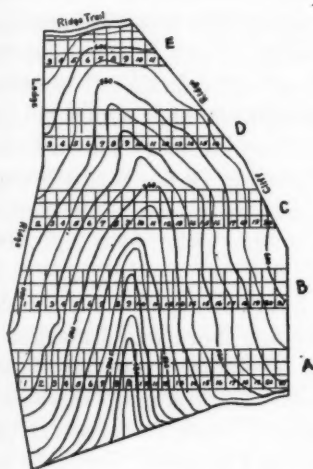spaced. The canopy of foliage was quite well developed and gen-

Oak.—hickory association.

White oak—sugar maple association.

Chinquapin oak—sugar maple
association.

Open glade associes.

Closed glade associes.

Fig. 11. Showing location of belt
transects.
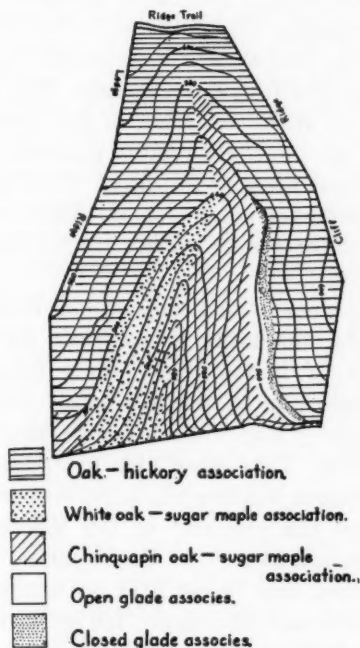
Fig. 12. Showing the tree associa-
tions of the area.

erally excluded the growth of a rich herbaceous flora on the forest
floor. The forest floor in all probability was carpeted with a thick
mat of litter, and a thick layer of humus lay on the soil surface. Such
forests, though they may be poor in herbaceous plant material dur-
ing the summer months, do, however, contain a rich herbaceous
spring flora. It is not unlikely that the early landowners took ad-
vantage of this fact and turned their stock into the forests in the
spring to forage on the fresh, succulent herbs. They were probably
also quick to learn that by burning away the thick mat of litter on

the forest floor, greater numbers of herbs could be induced to grow and that even certain grasses entered burned-off areas. Fire as an agent soon destroyed the layer of humus protecting the forest floor.

What little remained after the ravages of fire was stirred up by the cloven hoofs of the cattle, and, becoming an easy prey to the erosive power of heavy spring and summer showers, it was washed from the ridges and the slopes into the ravines and thence down to the river. Lacking the blanket of humus and litter the forest soils rapidly lost their moisture during the common late summer droughts. Competition for moisture among the trees became keen, many less sturdy individuals succumbing in order to balance this new deficit in water supply. The death of individuals left relatively large open "islands" in the forest canopy through which the rays of the sun could readily penetrate and thus intensify the xeric conditions already initiated. Continued grazing in the forest brought about even more erosion. More trees died, being unable to compete with their more sturdy kin for the necessary water with their roots bare.

A vegetational adjustment became imminent to prevent the complete denudation of the land. At this stage there was a marked influx of heliophilous plants formerly excluded from the forest. These plants, predominately red cedar *(Juniperus virginiana)*, slippery elm *(Ulmus fulva)*, and redbud *(Cercis canadensis)*, persisted. They were able to endure the late summer droughts and rigorous winters when the soil cover was scant. When the area became the property of the Missouri Botanical Garden grazing of forested areas was discontinued. The soil cover was no longer disturbed, and forest fires no longer reduced the protective layer of leaves and litter deposited by the trees each autumn. In a short time the heliophilous population matured, forming a lesser canopy of its own. Since the forest floor was shaded, a new carpet of humus and litter developed. The soil was once more cool and moist, permitting the origin and establishment of a new generation of the virgin flora. With this condition well in mind the complexity of the vegetation, previously referred to, becomes obvious when coupled with the wide range of habitats created by the geology, physiography and soils of the area.

An attempt was made to sort the various species into associations and associes on the basis of data secured from the graphs of the belt transects. However, the group of three heliophilous plants, previously referred to, appeared again as one to be dealt with be-

fore the true picture of the vegetational distribution could be composed. The density of the individuals comprising this group tends to mask any suggestions of association between the remaining species. The grazing conditions under which they have invaded the area and have become established have been discussed in considerable detail in a previous paragraph. In addition to these three species there may also be added: honey locust *(Gleditsia triacanthus)*, wild plum *(Prunus americana)*, black haw *(Viburnum rufidulum)*, and prickly ash *(Zanthoxylum americanum)*.

Three members of the heliophilous group tend to confine themselves to characteristic habitats, though, for the most part, they have a general distribution. Red cedar exhibits a decided preference for alkaline soils, and the oldest and healthiest specimens are to be found on the west slope of Cliff Ridge where the thin soil cover causes it to be influenced by the underlying dolomitic limestone rock strata. The black haw is essentially a small tree, loving open, rocky situations. The belt-transect graphs indicate it as being particularly distributed on the west slope of Cliff Ridge, where it has been shaded out by the more rapid growth of such large heliophilous trees as red cedar and slippery elm. Its present distribution is due to the open, xeric nature of the west slope of Cliff Ridge, maintained naturally by the southwestern exposure to the more or less drying, prevailing winds. It is probable that this area served as a center of distribution of the black haw to the east slope of Ledge Ridge and likewise to the pasture areas on either ridge. Prickly ash tends to prefer the more equable climate offered by habitats on the east slope of Ledge Ridge for it is here that fine mature specimens have developed. Like other members of this group, however, it will endure a wide variation in habitat and is rather generally distributed over the area.

With the above group of heliophilous plants withdrawn from consideration, the task of grouping the species into associations becomes comparatively easy. Inspection of the belt-transect graphs shows that it is possible to arrange the various genera and species of trees into three principal groups, two of which contain subordinate phases. A group, predominately oaks and hickories, shows decided preference for the ridges where it forms an oak-hickory *(Quercus-Carya)* association. Two developmentary phases are represented within this group. A second group dominated by white oaks and sugar maples, forming a white oak-sugar maple *(Quercus alba-Acer saccharum)* association, shows preference for the lower
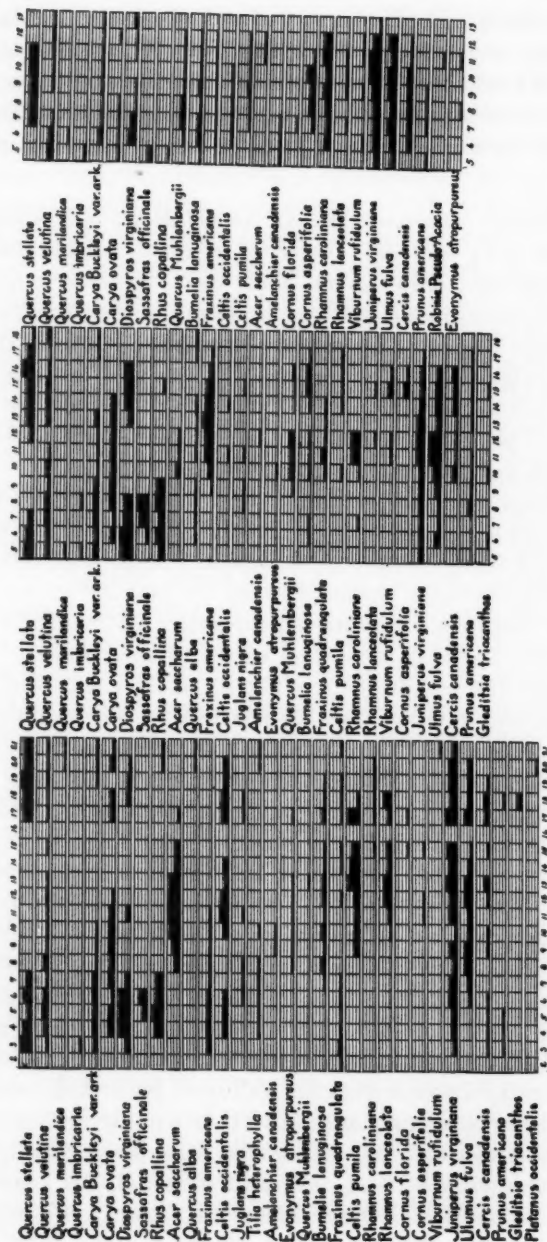
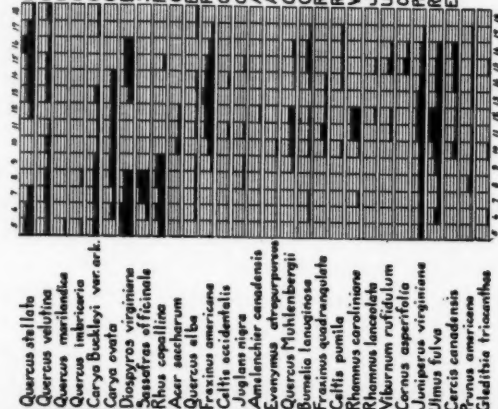Fig. 14. Showing distribution and density of species in belt transect B.

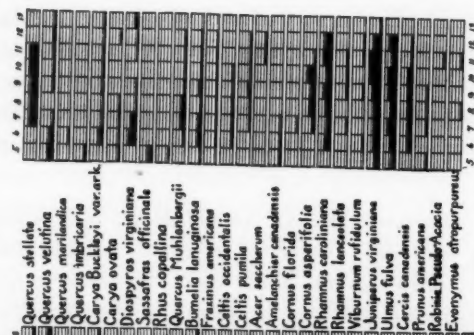Fig. 13. Showing distribution and density of species in belt transect A (see fig. 11).

Unit 1 = 0–1.4 plants; 2 = 1.5–2.4 plants; 3 = 2.5–4.4 plants; 4 = 4.5–7.4 plants; 5 = 7.5–11.4 plants; 6 = 11.5–16.4 plants; 7 = 16.5–22.4 plants; 8 = 22.5–29.4 plants.
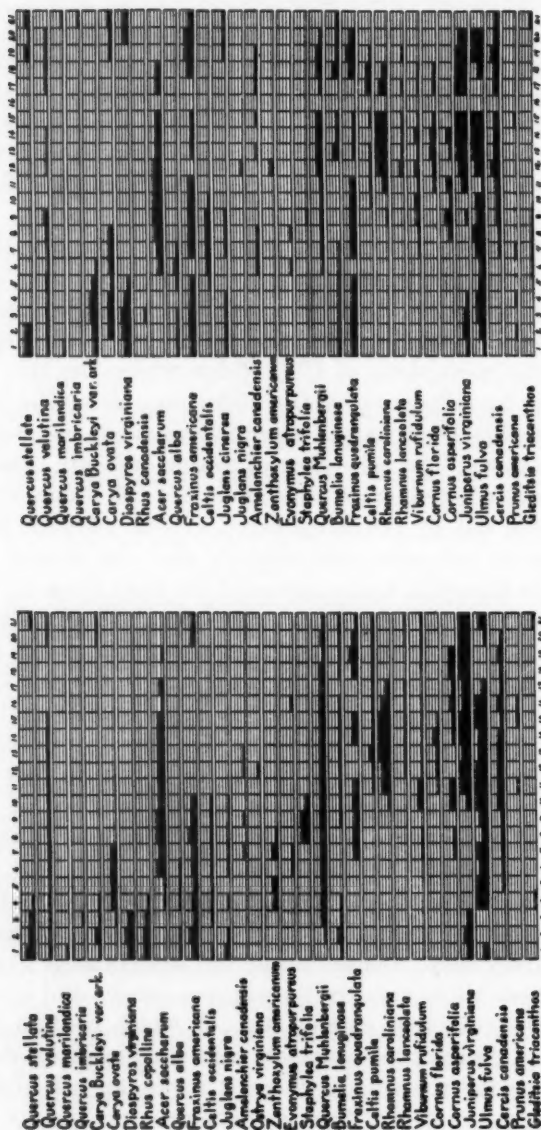
Fig. 15. Showing distribution and density of species in belt transect C.

Fig. 16. Showing distribution and density of species in belt transect D.

Fig. 17. Showing distribution and density of species in belt transect E.

slopes of Ledge Ridge. A third association is distinct in preferring the barren, rocky exposure of the west slope of Cliff Ridge. It is dominated by a growth of chinquapin oak and sugar maple. This association has a subordinate phase, a group of trees dominated by red cedar which prefers the more xerophytic environment of the glade.

The Oak-Hickory *(Quercus-Carya)* Association.—Grouped into this association are: post oak *(Quercus stellata)*, Ozark hickory *(Carya Buckleyi* var. *arkansana)*, black oak *(Quercus velutina)*, black jack oak *(Quercus marilandica)*, and the shingle oak *(Quercus imbricaria)* (figs. 13–17). The status of these trees within the association is not one of equal importance. A study of the belt-transect graphs indicates that the post oak and Ozark hickory are dominant. As stated above, these graphs are purely a study of density and distribution, and give no indications of size and age.

On Ledge Ridge and that portion of the ridge at the head of the valley, large trees are consistently white oak, black oak, and Ozark hickory. Judging from the ages of stumps of similar diameter elsewhere in the area their age varies between 150 and 200 years. This places them in that group comprising the relics of the virgin flora in which they may serve as indicators of the former climax.

On Cliff Ridge the conditions are not so easily read. The total deforestation of this portion (fig. 3c) has left no relic trees of the virgin forest. Although numerous stumps of trees, approximately 150–200 years old, are to be found, they were in a rather poor state of preservation and all that could be identified were oaks. The relatively great intervals at which the stumps occur seem to suggest that the trees were of stout, spreading habit such as that commonly developed by ridge-top post oaks. The probability of the former climax being composed essentially of post oak is supported by the fact that this ridge is for the most part very narrow. It receives little protection from hot dry winds by the surrounding ridges, and its high isolated position does not permit water to linger long either on or in the soil. Temperature recordings show that in summer this ridge is consistently warmer than the valley or lower habitats, and that during midday and early afternoon it is usually 5–8° warmer than a comparable station in the valley (fig. 8C). The present vegetation is predominantly of post oaks approximately 30 years old. Black oaks, white oaks, and Ozark hickories occur in minor numbers (figs. 13–17). Seedling trees are absent for the most part.

These facts seem to indicate the revival of a former post oak climax
on this ridge. Although post oaks also occur in great numbers on
Ledge Ridge (figs. 13–17), their distribution is different from that
observed on Cliff Ridge. On Ledge Creek it is almost totally limited
to the boundaries of the old deforested and pastured plot (figs. 3,
12), and exists as an associes, a stage leading to the development of
the oak-hickory climax association.[13] The belt-transect graphs
show a relatively high per cent of black oak, white oak, and Ozark
hickory also composing this old pasture flora (figs. 13–16). These
are, for the most part, young trees 5–10 years old, while the older
post oaks are 21 years old, a fact which indicates that the oak-hick-
ory climax common to Ozark ridges is rapidly becoming dominant.

An even earlier stage of the development in the succession from
cleared ridge lands to an oak-hickory climax association is repre-
sented by the pioneer plants, now almost completely dominated by
the post oak associes (fig. 12). Included in this "old field" associes
are persimmon *(Diospyros virginiana)*, sassafras *(Sassafras of-
ficinale)*, and shinning sumac *(Rhus copallina)*. With the exception
of the persimmon, which has a more general distribution, these oc-
cur as small "islands" only partially invaded by the more advanced
stage of the post oak associes. A comparison of the composite map
of the vegetation (fig. 12) with the map of the areal distribution of
the various degrees of soil acidity (fig. 6) shows a very close corre-
lation between the environment of these ridge-top trees and areas
of high degree of soil acidity. The white and black oaks of this as-
sociation have an indifferent attitude toward degree of soil acidity
and appear quite generally over the entire area. The remaining
members have distributional boundaries almost identical with the
areas of acid soils. These correlations support Steyermark's con-
clusions concerning the vegetation of the Ozarks in Missouri.[14] No
correlation could be found between this association and the soil
types (fig. 5), nor could it be identified with any particular outcrop-
ping of the various rock strata (fig. 2) which at this point are deeply
overlain with soil (fig. 4, a, b).

The White Oak–Sugar Maple *(Quercus alba–Acer saccharum)*
Association.—The belt-transect graphs reveal a second prominent
group of trees which conspicuously prefer the exposure of the east

[13] Steyermark, J. A. Studies of the vegetation of Missouri—I. Bot. Series, Field Mus.
Nat. Hist. 9: 351–475. 1940.
[14] Ibid., p. 405.

slope of Ledge Ridge (fig. 12). Unlike the neighboring ridge, this association is represented by a large group of species: white oak *(Quercus alba)*, sugar maple *(Acer saccharum)*, white ash *(Fraxinus americana)*, black oak *(Quercus velutina)*, shagbark hickory *(Carya ovata)*, hackberry *(Celtis occidentalis)*, burning bush *(Evonymus atropurpurous)*, black walnut *(Juglans nigra)*, shadbush *(Amelanchier canadensis)*, and bladder-nut *(Staphylea trifolia)* (figs. 13–16). As indicated in the discussion of the preceding association, it is not possible to assign dominance to any several species solely on the basis of facts represented in the belt-transect graphs. This association is fortunate in having a considerable number of virgin trees. A comparison of their trunk diameters with those of stumps of readable age elsewhere in the area places all of these trees between 160 and 200 years old, in that age class which is conspicuously composed of virgin trees. They are all straight-boled and form a relatively high canopy broken where many of them died out when the environment was altered by grazing. Of the large and older trees, white oaks and sugar maples are dominant. Aged, living sugar maples are not common in the area, probably because they were unable to endure the conditions brought about by grazing, namely, the depletion of the thick layer of litter and humus on the forest floor. The association has a well-developed understory of bladder-nut *(Staphylea trifolia)*, spice bush *(Benzoin aestivale)*, prickly ash *(Zanthoxylum americanum)* and burning bush *(Evonymus atropurpureus)*. Seedlings and saplings of white oaks and sugar maples abound.

An attempt to correlate this association with the various environmental factors reveals that it corresponds most closely with the limits of alkaline soils of the lower portion of the east slope of Cliff Ridge (fig. 6). This association prefers a pH range from 6.8 to 8.5. Here the degree of acidity of the soil is affected to a greater extent by the underlying dolomitic limestone because the soil layer is considerably thinner, varying from 8 to 14 inches in depth. The association may be further correlated with the limits of the "rough stony land" on this slope (fig. 5). The eastern exposure of the slope on which this association has developed has caused it to assume a mesophytic aspect. Being exposed to the east as it is, the slope receives the direct rays of the sun only in the morning before the air has been heated up. Thus the sun has a less burning effect upon the foliage of the trees during the summer drought periods. The slope is shaded from the rays of the sun during the heat of the day, from

2 to 4 p. m. The temperatures recorded on the slope are consistently from 1 to 4° cooler than those of a comparable position on the western slope (fig. 9C). The greater equability of this environment as compared with the distinctly xeric habitat on the west slope is manifest in a more succulent herbaceous flora. Humus and litter have collected in a thicker carpet on the forest floor, thus protecting it from excessive erosion and likewise serving as a moisture-conserving mulch.

The Chinquapin Oak–Sugar Maple *(Quercus Muhlenbergii–Acer saccharum)* Association.—As previously stated, this association inhabits the western slope of Cliff Ridge (fig. 12). The dominant trees are chinquapin oak *(Quercus Muhlenbergii)* and sugar maple *(Acer saccharum)*. Other important members of the association are: red cedar *(Juniperus virginiana)*, chittim-wood *(Bumelia lanuginosa)*, black oak *(Quercus velutina)*, and blue ash *(Fraxinus quadrangulata)*. Trees playing a minor part in the association are white ash *(Fraxinus americana)* and black walnut *(Juglans nigra)*. Trees and shrubs forming the rich understory are: dwarf hackberry *(Celtis pumila)*, redbud *(Cercis canadensis)*, Indian cherry *(Rhamnus caroliniana)*, black haw *(Viburnum rufidulum)*, buckthorn *(Rhamnus lanceolata)*, flowering dogwood *(Cornus florida)* (figs. 13–16).

The association has a light, open aspect, no canopy in a true sense having been developed. Relatively few of the dominant trees are actually dead though many exist in a poor state of health. A comparison of the trunk diameters with stumps of known age places the majority of the older specimens in the group of virgin trees. The habit of these trees seems to suggest that the aspect of this association has not been appreciably altered by grazing conditions. The fact that these trees have a lower and more spreading branching habit than that of the typical forest specimens in the associations previously described indicates that they developed under conditions very similar to the semi-xerophytic ones existing today, and may perhaps account for the slight damage suffered from grazing.

It is probable that even prior to the advent of human activities in the area, the soil cover lay thin on the bed rock beneath, and that though a rather rich herbaceous flora had developed it was necessarily xerophytic in nature. These facts are in accord when one remembers that the western exposure of this habitat leaves it relatively unprotected from hot, dry south and southwestern summer

winds, and likewise raw, cold winter winds. The attitude of the slope causes it to have a high angle of incidence to the rays of the sun during the heat of the day, that is, from 2 p. m. to 4 p. m. This results in a temperature of 1–4° over that recorded at a comparable station on the east slope of Ledge Ridge (fig. 9). This xeric condition is intensified when the numerous thin-bedded phases and sand lenses incorporated in the rock strata are taken in consideration (fig. 1). These serve as drains through which percolating ground waters are rapidly conducted off, leaving little water in reserve for periods of drought despite the high organic content of the soil. As previously mentioned, the shallow depth of the soil has caused it to be exploited to a high degree by roots of trees and herbs, which necessarily means that it would be rapidly depleted of moisture regardless of the high content of organic matter. The relatively thin depth of the soil layer, together with its residual origin from the underlying dolomitic limestones, has favored the development of a typically alkaline soil (fig. 6) which is reflected markedly in the flora. Steyermark includes the dominant plants of this association in his list of plant indicators of alkaline soils.[15]

The Glade Associes.—The glade is a plant environment distinct from all other habitats presented by the area (fig. 1). The soil is very shallow, and numerous rock shelves are exposed, which, together with the conspicuous lack of trees over the greater part of its extent, give the glade a barren open aspect. Further inspection shows the position of the glade to be correlated with the extent of the outcropping of the upper, thin-bedded phase of the Cotter formation on this western slope. This suggests that the origin of the glade lies within the properties of this rock. In a previous paragraph this thin-bedded phase of the Cotter formation was characterized as being a highly porous and permeable rock. These features and the comparatively great depth, 7 feet, of this phase cause it to present a plant habitat with a wide range of seasonal conditions. The high porosity and permeability of the rock permit free movement of water. Early spring rains rapidly percolate through the rock or water may be drawn from it by rapid evaporation, having been brought to the surface by capillary action. This means that the rock creates an arid substratum during summer. In autumn and late winter another extreme is experienced. With the increase in precipitation and accompanying decrease in evaporative powers of

[15] *loc. cit.*, p. 407.

the atmosphere, the rock becomes literally saturated with percolating ground water. The sparse plant cover does not bind the soil in place against spring and later summer rains (fig. 7). The surplus of water in the bedrock beneath the soil in winter forces its way to the surface of the rock, where, acting as a lubricant and erosive agent, it also carries the soil away. The western exposure of this unique environment only tends to intensify the already extreme edaphic conditions. In summer the hot, dry, southern and southwestern winds, and the high angle of incidence of this slope to the rays of the sun during the heat of the day, create intensely desiccating conditions.

The Open Glade Associes.—Almost the entire area of the glade is open (fig. 12), appearing like a barren, rocky, upland meadow. These conditions have resulted in almost total exclusion of an arborescent flora. Over the greater part of its extent an herbaceous associes prevails, Missouri black-eyed Susan–bluestem *(Rudbeckia missouriensis-Andropogon scoparius)*. Trees are excluded from the open glade, the arid summer conditions preventing the establishment of seedlings. However, several small "islands" of red cedars are trying to exist here.

The Closed Glade Associes.—The small closed glade is founded on essentially the same environmental conditions as those controlling the open glade. However, it differs from the open glade in being forested with a red cedar *(Juniperus virginiana)* associes. Other important trees are: chinquapin oak *(Quercus Muhlenbergii)* and chittim-wood *(Bumelia lanuginosa)*. A well-developed understory is composed of Indian cherry *(Rhamnus caroliniana)*, buckthorn *(Rhamnus lanceolata)*, dwarf hackberry *(Celtis pumila)*, black haw *(Viburnum rufidulum)*, redbud *(Cercis canadensis)*, and flowering dogwood *(Cornus florida)*. This associes is distributed as a narrow band bordering the upper edge of the open glade associes (figs. 1, 12), and may be correlated with the uppermost portion of the thin-bedded phase of the Cotter formation and the basal sandy phase of the Powell formation (figs. 2, 12). Here the substratum of rock remains more moist since it lies adjacent to the massive rocks of the Powell formation which retains percolating ground waters considerably longer than the thin-bedded cotton rock of the Cotter formation. Humus is washed down upon the glade from the oak woods above it and is an important factor in increasing the soil moisture since it serves as both a reservoir of

moisture and as a mulch. This increase in soil moisture has permitted the invasion of trees upon the glade edge. The extremely xeric conditions prevailing during the summer months, however, limits the habitat to occupation by drought-resistant species such as red cedar, chittim-wood, and chinquapin oak. Though a canopy of interlacing cedar boughs is well developed it is characteristically of a gauze-like texture, and permits abundant light to encourage the rich understory of small trees and shrubs.

These glade associes have, in all probability, been the least injured by grazing. The xerophytic nature of the open glade necessarily produces plants of a tough, leathery texture which offers little encouragement to cropping by animals. A thick mat of slowly decaying cedar needles prevents seeds of herbs from reaching a suitable stratum for germination. Thus it is evident that this associes was undisturbed by livestock. A portion of the associes was deforested (fig. 3c), but this caused little alteration of the flora aside from the removal of the virgin trees. Steyermark has shown how similar glades and rocky barrens in the Ozarks are invaded and dominated in part by red cedar and chittim-wood among other trees.[16] Dead or dying specimens are almost totally absent. It is evident that this associes exists today much as it must have before settlement of the region by white man.

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[16] *loc. cit.*, p. 372–377.

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HELMINTHOSPORIUM SPOT OF CITRONELLA AND LEMON GRASS IN GUATEMALA

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During August, 1941, a severe epiphytotic developed on citronella *(Cymbopogon Nardus* (L.) Rendle subspec. *genuinus)* and lemon grass *(Cymbopogon citratus* (DC.) Stapf) at Los Cerritos, a very large plantation near the upper edge of the coastal plain below Escuintla in Guatemala. The weather had been somewhat abnormal, with earlier light rains and higher humidities at the end of the preceding dry season, although the rainfall for the whole subsequent rainy season was not conspicuously high. Owing to the increased demand for essential oils, the plantation had been irrigated throughout the dry season instead of cutting off the water for the last two or three months as in previous years. This kept the trash and marcescent leaves at the bases of the plants moist for the production of a larger number of spores while the higher humidities probably aided in securing more abundant germination and infection. By the end of August all but the very young leaves had died back about half their length, and the distilling plant was closed for about six weeks for the first time since the plantation came into production about ten years before.

An examination of a large number of plants showed that the principal damage resulted from a leaf spot, although an occasional plant of citronella showed a rot associated with *Fusarium* sp. at the bases of the stems a short distance above the soil. The leaf spot begins as a small yellowish area between the veins. It develops more rapidly between the veins than across the smaller ones, resulting in an elliptic to nearly linear area of necrosis with a reddish margin, quite similar in appearance to the *Helminthosporium* leaf spot of sugar cane. The central portion soon becomes brown and dry, but does not drop out. As the spots increase in number, evidently the water supply is reduced and the distal portion of the leaf slowly

wilts and dies. Transverse sections of the leaf through a leaf spot apparently show cross-sections of thick-walled, brownish hyphae in the phloem of the bundle next the leaf spot, with the whole phloem area brown and necrotic. The dead tissue may then be invaded by saprophytes such as *Hormodendrum*.

The *Helminthosporium* was easily isolated on Thaxter's potato-glucose agar and grows equally well on Sabouraud's glucose agar, although on both media the spores are somewhat smaller (24–35×8–15.5 μ, average 29.5×12.4 μ) than when developed on the host (46–54×18–24 μ, average 49×20 μ). The strain on lemon grass has somewhat smaller spores (19.5–28.6×7–15 μ, average 25.8×10 μ) than those of the citronella strain, but further study will be necessary to determine whether the difference is significant as no morphological differences have been noticed.

On the host, the conidia develop at the tip of a short, stiff conidiophore. As the first spore develops, the supporting cell proliferates dichotomously and produces a second spore. This may be repeated, giving about three spores in a compact group at the tip of the conidiophore as in *Acrothecium* (pl. 13, fig. 8). The mature spore is asymmetric, flattened on one side or somewhat curved, with one cell (usually the subterminal) much larger than the others.

In agar colonies, conidia are borne singly, both terminally and laterally (pl. 13, figs. 5, 10, 11), as well as in a terminal group on short lateral branches corresponding to the conidiophores on the host (pl. 13, figs. 6, 11). In the original cultures on potato-glucose agar, the large subterminal cell of the conidium often proliferated laterally, producing a mature spore suggestive of the staurospore found in *Triposporium* Corda (pl. 13, figs. 4, 6, 11). This type of spore has not been seen in subcultures on Sabouraud's glucose agar, prepared from the original cultures after six months.

The systematic position of this organism is not altogether clear from the limited literature at my disposal. The staurospores are considered as abnormal since I have found them only in cultures on potato-glucose agar, and may result from some morphogenetic stimulus in the medium. The grouping of spores at the tip of the conidiophore suggests *Acrothecium* Preuss but is believed to result from a different ontogeny, similar to that of *Helminthosporium Sacchari* (Breda da Haan) Butler, if the internodes between spores were greatly shortened and the spores were less caducous. *Brachysporium* Saccardo and *Napicladium* Thuemen resemble our organism in many respects, but their distinction from *Helmintho-*

sporium Link is not clear. Hence in the absence of further information regarding this group of genera, I have preferred to describe the species in the oldest genus.

HELMINTHOSPORIUM **Cymbopogi** Dodge, sp. nov.

Conidiophori rigidi, erecti, fumosi vel obscure brunnei, septati neque ad septa constricti neque ramificati; conidia 3–5-septata, terminalia, singula vel in capitulis parvis, asymmetrica, uno latere applanata aut leviter curvata, 46–54 × 18–24 µ.

Conidiophores rigid, erect, smoky or dark brown, septate, not constricted at the septa nor branched; conidia with 3–5 thick, transverse septa, terminal, single or in small groups, asymmetric, flattened on one side or slightly curved, thick-walled, usually with the penultimate cell much larger than the others, 46–54 × 18–24 µ.

Guatemala: Escuintla, Los Cerritos, *Dodge,* on citronella, TYPE; same locality and collector, on lemon grass.

The spore germinates from the basal cell by a tube which pushes between the epidermal cells until it is below the thicker portion of the wall of the host cell, then penetrates the epidermal cell (pl. 13, fig. 7). If the tube fails to penetrate, it forms a dichotomously branched mycelium (pl. 13, figs. 1, 9).

Preliminary experiments indicate that this disease may be controlled by spraying with either Bordeaux mixture or lime-sulfur. A promising beginning has been made in the selection of resistant clones. Two clones with a relatively small amount of infection in a very heavily infected area were selected, divided into the usual seed bits and planted in a freshly prepared section of the plantation. As they mature for the first cutting, about half of them are relatively free from infection. The other half and the surrounding area are again heavily infected, as this area has not yet been sprayed owing to lack of adequate equipment for spraying such a large plantation. It is hoped to carry this selection further, since in normal times the cost of spraying is so great that it will be impossible for Guatemalan farmers to compete with those in other regions with much lower labor costs.

EXPLANATION OF PLATE

PLATE 13

Fig. 1.   Germinating spore of *Helminthosporium Cymbopogi* Dodge, strain on citronella.

Fig. 2.   Terminal group of conidia, strain on lemon grass, from cultures.

Fig. 3.   Younger stage of the above. The older spore on the right has already thickened its walls, while the younger one on the left has just produced transverse septa.

Fig. 4.   Conidia of the strain on lemon grass from potato-glucose agar culture.

Fig. 5.   Single terminal conidium of the strain on lemon grass from potato-glucose agar culture.

Fig. 6.   Group of conidia, strain on lemon grass from potato-glucose agar culture. This hypha is more moniliform than the usual hyphae in cultures.

Fig. 7.   Germinating conidium, showing method of penetration of the citronella leaf epidermis.

Fig. 8.   Conidiophore and group of conidia on leaf of citronella.

Fig. 9.   Germinating conidium of lemon grass strain from culture.

Fig. 10.   Very young terminal group of conidia of lemon grass strain; only the first spore has thickened its walls, the second spore has divided only once, while the two youngest spores have not begun to divide. A young spore is forming laterally below.

Fig. 11.   Various types and groupings of conidia of the citronella strain from potato-glucose agar culture along a single hypha.

Plate 13
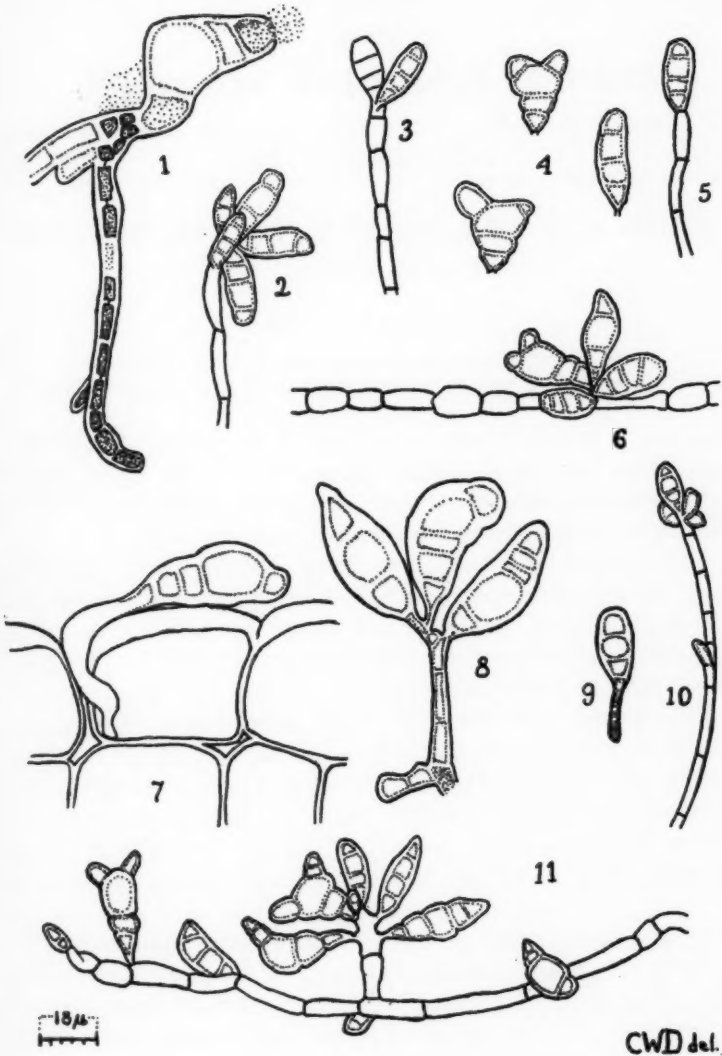
CWD del.

DODGE—HELMINTHOSPORIUM CYMBOPOGI